

**Subtidal Macroalgal Studies in East and South Eastern  
Tasmanian Coastal Waters.**

by  
John Craig Sanderson  
B. Sc. (Melb. Uni.)  
B. Sc. Hons. (Uni. of Tas.)

Submitted in fulfilment of the requirements for the degree of  
Master of Science, Department of Plant Sciences,  
University of Tasmania, May 1990.

## DECLARATION

This thesis has not been submitted for the award of any other higher degree or graduate diploma in any tertiary institution and to the best of the authors knowledge contains no material published or written by any other person without due reference in the text.

JC Sanderson

## ABSTRACT

This thesis is concerned with (1) the introduced Japanese macroalga *Undaria pinnatifida* in Tasmania and (2) the growth patterns of major components of macroalgal communities at two sites on Tasmania's coast, Bicheno in the east and George III Reef in the south. The algae studied were *Macrocystis pyrifera*, *Ecklonia radiata*, *Phyllospora comosa* at both sites plus the red algal community at George III Reef.

Surveys of *Undaria* in 1988 found that it inhabited approximately 15 kilometres of the east coast from Triabunna southwards to Lachlan Is. The alga is very fecund and smothers the bottom in 'barren' areas particularly in sheltered waterways at certain times of the year. Effects on the local biota are unknown but the environmental tolerances of the alga reveal a potential distribution from Cape Leeuwin in south west Western Australia to Wollongong on the New South Wales Coast.

Environmental parameters and growth rates were monitored at George III Reef from 1985-88 and at Bicheno from 1987-88. Over the joint period, there was little difference in temperature, salinity and nutrients of the seawater between the two sites.

In 1988, the water masses of the south and east coasts of Tasmania were distinguished by unusually warm waters. In March, the warm nutrient - depleted waters of the East Australian Current were detected further south than usual and in winter, coastal waters were relatively warm and nutrient poor compared to previous years (Harris et. al 1991).

For *Ecklonia radiata*, light appears to be the most significant factor affecting the rate of increase in lamina length and thus production at Bicheno and George III Reef. At George III Reef, high temperatures and

to a lesser extent large swells negatively affect growth rates. It is postulated that swell may be acting indirectly through its affect on the amount of suspended particles in the water column and thus reducing light. Productivity estimates suggest 1.8 kg wet wt/m<sup>2</sup>/yr at 14m depth at George III Reef and 4.7 kg wet wt/m<sup>2</sup>/yr at 10 m. depth at Bicheno in areas of continuous cover.

For *Macrocystis*, production appears to be best determined from rate of blade production because change in length may be affected extrinsically by factors of swell and light. Productivity of *M. pyrifera* at the two sites suggests similar frond productivities of 6 kg wet wt/frond/yr. For a typical density of 4 fronds per m<sup>2</sup> of sea floor this results in estimates of 24kg wet wt/m<sup>2</sup>/yr weight. *Macrocystis* disappeared almost entirely from both sites during the warm year of 1988.

For *Phyllospora*, regression of growth increment against environmental parameters indicates light availability as the principal factor affecting growth for most of the year though nutrients are likely to limit growth in late summer. High rates of plant mortalities and lower growth rates late in the study coincide with the incursion of the EAC and the warm winter of 1988. The calculated production at George III Reef of approximately 7.4 kg wet wt/m<sup>2</sup>/yr at 7.7m depth compares with the combined *Phyllospora comosa* and *Ecklonia radiata* annual production figure of 4.8 kg/m<sup>2</sup>/yr at Bicheno at 10m depth.

For the red algal community at George III Reef, filamentous and foliose species increasing in number in the summer and outside of the *Macrocystis* canopy. The presence of the *Macrocystis* canopy results in a halving of the red algal biomass/m<sup>2</sup>.

## ACKNOWLEDGEMENTS

Thankyou to the late Charlie Pearson for technical assistance and keeping 'SS Research' afloat and running for the period of the study.

Thankyou to Dr. David Thomas and Dr. Bob Hill for constant encouragement and support.

Thankyou to my eventual supervisor Dr. Peter Tyler.

Thankyou to other members of the University of Tasmania Botany Department for sundry assistance.

Thankyou to people at CSIRO Marine Laboratories including Harry Higgins, Ron Pleschke, Gary Critchley and Lesley Clementson.

Thankyou to the staff at the Army Food Science Laboratories for time and assistance.

Thankyou to members of the 'A' (abalone) Team at the Department of Sea Fisheries for their help on the many trips to George III Reef.

Thankyou to Harry Higgins and Dr Hugh Kirkman for discussions in the early stages of the project.

Thankyou to Dr Jeremy Prince for providing the springboard for the initiation of the study and continued support for the duration.

Thankyou to members of the University of Tasmania SCUBA Club for 'buddies' on dives to George III Reef and Bicheno including in particular; Rudy Kloser, Garry Davidson, Dot Stean, Remo Di Benedetto and Neville Barrett and others including Andrew Cawthorn, Steven Trebeck, Simon Talbot and Jamie Whitworth.

Thankyou to Fiona Garrigan for her support and patience in the latter stages of the study.

Last, but certainly not least, thankyou to my parents, John and Jimmy Sanderson for support, assistance, faith and patience over the lengthy period of my intermittant academic career.

## CONTENTS

	<i>Page</i>
TITLE PAGE	
ABSTRACT	
ACKNOWLEDGEMENTS	
DECLARATION	
TABLE OF CONTENTS	
 PART 1. A Survey of the Distribution of the Introduced Japanese Macroalga <i>Undaria pinnatifida</i> (Harvey) Suringer in Tasmania.	
INTRODUCTION	1
TABLE AND FIGURES	21
 PART 2. Growth of Macroalgae at Two Sites on the East and South-Eastern Coasts of Tasmania.	
 CHAPTER 1: Introduction	33
 CHAPTER 2: The Coastal Environment.	
INTRODUCTION	59
TABLE AND FIGURES	70
 CHAPTER 3 : <i>Ecklonia radiata</i>	
INTRODUCTION	95
TABLE AND FIGURES	114
 CHAPTER 4 : <i>Macrocystis pyrifera</i>	
INTRODUCTION	126
TABLE AND FIGURES	147
 CHAPTER 5 : Transplant and Development of Juveniles of <i>Ecklonia radiata</i> and <i>Macrocystis pyrifera</i> .	
INTRODUCTION	158
FIGURES	168
 CHAPTER 6 : <i>Phyllospora comosa</i>	
INTRODUCTION	180
FIGURES	194
 CHAPTER 7: The Red Algal Community at George III Reef.	
INTRODUCTION	210
FIGURES	224
 CHAPTER 8: Macroalgal Growth in Tasmanian Waters	
INTRODUCTION	233
FIGURES	244
 CHAPTER 9: Potential Factors Affecting Abalone Distributions in Tasmanian Coastal Waters.	
INTRODUCTION	245

REFERENCES	251
APPENDIX 1. Transect results for <i>Undaria</i> survey.	269
APPENDIX 2. Results of <i>Undaria</i> maximal cover harvested quadrats.	274
APPENDIX 3. Species list with authorities for George III Reef.	275
APPENDIX 4. Results for summer and winter harvested quadrats of <i>Ecklonia</i> and <i>Phyllospora</i> .	278
APPENDIX 5. Permanent quadrat data.	280
APPENDIX 6. Species-area quadrat data.	291
APPENDIX 7. Harvested quadrat data.	296
APPENDIX 8. Harvested <i>Durvillaea potatorum</i> at George III Reef.	299

## PART 1

# A Survey of the Distribution of the Introduced Japanese Macroalga *Undaria pinnatifida* (Harvey) Suringer in Tasmania.



## PART 1, CHAPTER 1.

### THE INTRODUCED JAPANESE MACROALGA UNDARIA PINNATIFIDA (HARVEY) SURINGER IN TASMANIA, 1988.

#### INTRODUCTION

On January 29, 1988, several specimens of the plant *Undaria pinnatifida* were found on the beach at Rheban on Tasmania's east coast. This species was originally an endemic to Japan and adjacent coasts. Recently however, plants have been found in France at Etung de Thau (1971, Perez *et al.* 1984) and Wellington Harbour, New Zealand (1987, Hay and Luckens 1987). Introduction of the plants to France is believed to have been with spat of the Japanese oyster, *Crassostrea gigas*, and to New Zealand via Japanese fishing boats.

The most likely vector for the introduction of this alga to Tasmania is the ballast waters of ships that transport woodchips to Japan from a mill at Triabunna, Tasmania (Sanderson and Barrett 1989; Sanderson 1990). Anecdotal evidence of divers suggests that introduction may have occurred as early as 1982 (J. Bostock pers. comm.). A survey was conducted in December 1988 to determine the extent of distribution, approximate quantities, the rate of further infestation and likely long term affects. The survey was initiated in response to complaints from abalone divers who were finding it difficult to locate abalone amongst the cover of *Undaria pinnatifida*, in the Mercury Passage near Triabunna.

## METHODS

To determine aspects of the biology of this alga, a literature search was conducted. Contact was also established with phycologists dealing with 'invasions' by *Undaria* in New Zealand (Dr Cameron Hay, DSIR, NZ) and France (Dr I. Wallentinus Dept. of Botany, University of Goteborg, Sweden). Dr I. Wallentinus was nominated by ICES (International Council for the Exploration of the Sea) to report on the likely effects of the introduction of *Undaria* to Europe for the Working Group on Introductions and Transfers of Marine Organisms.

The probable extent of distribution was initially established through contact with local abalone divers, J. Bostock and H. Wright, and from the results of a less comprehensive survey conducted in August 1988 (Sanderson and Barrett 1989). In December 1988, 'Drop' dives were undertaken to confirm the geographical limits of distribution and a number of transects running perpendicular to the shore were conducted to determine distribution of the alga with depth for a variety of different exposures to wave action (Figs 1-2). The briefer survey in August 1988 showed that plants in the vicinity of the Woodchip Mill were at a more advanced stage of maturity than the plants further south. Plants in the vicinity of the Mill were past their maximum size at the time of this later survey. Southern plants were still close to maximal. As the intent was to estimate maximal levels of plant biomass, transects were done only south of the Mill. A transect was also conducted at Long Point on Maria Is. This was not as yet an infected area but the likelihood of future infection was judged to be high. A transect was conducted here for comparative purposes. Other dives had been conducted throughout 1988 and the results of these observations have been incorporated in this study.

On each transect, percentage cover of different plant species, in particular *Undaria*, and the numbers of urchins and limpets were estimated at regular depth intervals. Urchin and limpet numbers were noted to show possible correlations. Note was also taken of various physical parameters for the transects and at each of the depth intervals. These included; aspect, a subjective estimate of exposure to wave action, and at each depth interval, a substrate description, i.e. whether Reef (Re), Boulders (B) or Sand (S). More statistically rigorous sampling was not undertaken due to time and money constraints. The intention of this study was only to give an indication of approximate quantities and to describe the alga's habitat.

One square metre of *Undaria* was harvested at each of the regular depth intervals in an area of continuous cover, these samples were weighed and the number of plants counted.

At Emerald Bay (Fig. 2) on December 3, 1988, plants were collected from 2, 4, 6 and 8 m depths and returned to the laboratory for basic morphometric measurements of length and wet weight. Emerald Bay differed from other sites as there *Undaria* was the dominant alga from Mean Low Water through the entire depth range to 12 m.

Sporophylls of some mature plants were returned to the laboratory and spore release was effected according to standard methods (eg. Stein 1973, Novacek 1984c, Yoneshigue and Oliveira 1987). Spores were cultured in PES medium and maintained at 17°C with the medium changed weekly.

## LITERATURE SURVEY

The potential areas for distribution of seaweeds depends on their physiological tolerance limits, i.e. ranges of temperature, salinity, light intensity, light regimes, nutrient availability, and on substrate for attachment. In a geographic area corresponding to these requirements, the

existence of a species further depends on the availability of spores, competition with other species for space, light and nutrients, on grazing and how completely the parts vital for growth and reproduction of the alga are grazed. Table 1 indicates some of these limits for *Undaria* as obtained from the literature.

**Table 1.** Performance of *Undaria pinnatifida* with regard to different factors as determined from the literature.

#### PHYSIOLOGICAL TOLERANCES/OPTIMA

##### TEMPERATURE

###### Growth of sporophyte

15-17°C- optimal for young thalli,	Saito 1975
<12-13°C- opt. for older thalli, 15-20°C-slower growth	Arasaki & Arasaki 1983
10-15°C (opt.), >20°C -degradation, >23°C -death.	Akiyama 1965
10-20°C -opt young thalli.	Bardach <i>et al.</i> 1982
10-15°C	

###### Release of zoospores

7-23 °C	Akiyama and Kurogi 1982
14-23°C (opt 17-22°C)	Saito 1975
>14°C	Bardach <i>et al.</i> 1982
17-20°C	Arasaki & Arasaki 1983

###### Growth of gametophytes and release of gametes

15-20°C growth; maturity <20-23°C	Bardach <i>et al.</i> 1982
10-20°C possible, survival -1-27.5°C	Akiyama 1965
17-24°C opt. growth, possible 15-24°C, survival -1-30°, Maturity 8-15°C	Saito 1975.

##### SALINITY

###### Growth of sporophyte

(27-)30-33 g/l	Bardach <i>et al.</i> 1982
> 27 g/l	Saito 1975

###### Attachment of zoospores

18-33 g/l	Saito 1975
-----------	------------

###### Maturity of gametophytes

(27-)20-33 g/l	
>27 g/l	Saito 1975

##### LIGHT INTENSITIES

###### Sporophyte

500-3000 lux	Saito 1962
low light int. at high temp. and higher intensities at lower temperatures	Saito 1975
light compensation 100 lux and light sat. 18000 lux	Wu <i>et al.</i> 1981

<b>Growth and maturity of gametophytes</b>	
570-4000 lux	Akiyama 1965
>150 lux	Saito 1975
1000 lux(opt)	Akiyama and Kurogi 1982
<b>LIGHT-DARK REGIMES</b>	
<b>Sporophyte development</b>	
short day	Saito 1975
short day or long day	Akiyama 1965
<b>Gametophyte development</b>	
short day	Saito 1975
long day	Akiyama 1965
<b>NUTRIENT REQUIREMENTS</b>	
none as yet determined.	
<b>SUBSTRATE REQUIREMENTS</b>	
Hard substrate, natural or artificial	All references
<b>WATER MOVEMENTS</b>	
< 8 cm/sec for zoospore attachment	Saito 1975
<b>ECOLOGICAL PERFORMANCE</b>	
<b>GEOGRAPHICAL DISTRIBUTION</b>	
Asia:	
Japan - most suitable coasts excl N and E Hokkaido	Saito 1975
Korea N & S	
China; Quing dao, Shidao, Yantai, Dalian Zhejiang	Zhang <i>et al.</i> 1984
USSR; Vladivostok, Okhotsk Sea	Funahashi 1974
Europe; France; Mediterranean Sea	
(l'Etang de Thau, Port-la-Nouvelle)	Bouderesque <i>et al.</i> 1985a
New Zealand; Wellington, Timaru	Hay pers. comm.
<b>DEPTH RANGES</b>	
Japan lower intertidal- 15 m	Saito 1975
Europe; Mediterranean Sea -5 (18) m	Floc'h <i>et al.</i> 1991.
<b>SPOROPHYTE APPEARANCE</b>	
Asia; Korea E coast; Dec.	
Japan; NE Honshu Oct.-Nov.	Akiyama & Kurogi 1982
Europe; France; Mid Nov.-March	Perez <i>et al.</i> 1981-1984
<b>SPOROPHYTE MATURITY</b>	
Asia; Japan SE Hokkaido; June -July	
NE Honshu March - July	Akiyama & Kurogi 1982
Europe; France; Mediterranean; May- June	Perez <i>et al.</i> 1981 1984
<b>SPOROPHYTE DISAPPEARANCE</b>	
Asia; Korea E coast; June	Akiyama & Kurogi 1982
Japan; July-Aug	Arasaki & Arasaki 1983.
Europe; France; Mediterranean June-July	Perez <i>et al.</i> 1981, 1984

#### SIZE OF SPOROPHYTES

Asia; Korea; 1-2 m	
Japan; 1-2 m	Akiyama & Kurogi 1982
China; 1-2 m	Zhang <i>et al.</i> 1984
Europe; France; 0.7-1.3 m	Perez <i>et al.</i> 1981
New Zealand; 0.7-1.3 m	Hay & Luckens 1987

#### COMPETITIVE ABILITY

Japan; < 15% frequency in Laminaria beds	Sakai 1977
Deposition of stones on the sea bed and blasting of rocks imply dependence of new substrate for growth	Saito 1975
France; mainly on artificial substrates	Boudouresque <i>et al.</i> 1985a
NZ; variety of substrates favouring bare areas	Hay 1988

#### Introduction to France.

*Undaria* was first discovered in France in 1981. It was accidentally introduced in the l'Etang de Thau, Sete, on the French Mediterranean coast in 1981 with oysters from Japan. In 1983, field tests of plantings of *Undaria* were carried out on the French Atlantic coast at Ile de Groix, Ile d'Ouessant and St. Malo, on the Rance Estuary to assess the potential for establishing an industry based on *Undaria*. The promoters started the farm in the belief that;

1/ the sporophytes would grow better in cold water and

2/ *Undaria* would not be able to reproduce *in situ* on the Atlantic coast because the temperatures would be too low for the female gametophytes to reach maturity and thus be confined to the farm site (Perez *et al.* 1984, Floc'h *et al.* 1991).

The farm grew the alga successfully with "les resultants spectaculaires" in 1983 and 1984. In 1985 a working group on the Introductions and Transfers of Marine Organisms established for the ICES (International Council for the Exploration of the Sea), in consideration of this venture, passed a resolution stating, "any commercial cultivation and expansion of the existing pilot project of *Undaria* be held in abeyance. Also that an extensive study and risk assessment be undertaken of *Undaria* in the likelihood of escape."

The *Undaria* cultivation program was subsequently reduced to Ile d'Ouessant. A two year ecological study of *Undaria* was started in January 1987 by Dr J. -Y. Floc'h and M. R. Pajot. The aims of the study were to monitor the spread of the *Undaria* and to conduct manipulative experiments focusing on its competitive abilities and resultant changes in grazing pressures.

In 1987 *Undaria* sporophytes were found at Ile d'Ouessant growing vigorously on immersed supporting structures, old and newly built. A few plants were also recorded from rocks to a depth of -5 (-18) metres (Floc'h *et al.* 1991). The claims put forward by the algal promoters originally were erroneous. An examination of the critical temperatures for zoospore release and germination in Table 1 demonstrates the wide limits given by different scientists and in fact supports the hypothesis that the species can indeed produce zoospores, germinating into gametophytes at temperatures likely to be experienced on the coast at Ile d'Ouessant (10-17°C, van den Hoek 1982).

ICES recommendations regarding future cultivation of the species on the Atlantic coasts of Europe have not yet been published. Details of experiments on competition between *Undaria pinnatifida* and local algae also have not yet been released although the plant does not seem to be very competitive, especially if compared to *Saccorhiza polyschides* (Floc'h *et al.* 1991).

#### New Zealand introduction

*Undaria* was first discovered in New Zealand in Wellington Harbour in August, 1987. Since then it has been discovered growing at a number of Ports including Timaru, Oamaru and Lyttelton, along 500 km of coastline. Hay and Luckens (1987) speculate that introduction to Wellington may have been via Japanese and Korean squid boats. At Timaru, circumstantial evidence indicates these same fishing boats to be the source as the plant is

believed to have arrived shortly after the Timaru Harbour Board began cleaning Japanese squid boats (Hay 1990).

A significant find by Dr. C. Hay is the ease of dispersal by local boats. After fishing boats initially moored at Timaru had motored to Oamaru, a harbour 50 miles south, they were found to have healthy individual plants attached to their hulls; these had established themselves while the boats were still at Timaru. The New Zealand Oceanographic Research Vessel 'Rapuhia' steamed 4000 km between the 15 November and 13 December 1989 and sporophytes found attached before leaving were still there on the boat's return, in fact their average length had increased to 20-30 cm. At Lampton Harbour in Wellington the kelp has been found growing on the hulls of 25% of moored pleasure craft (Hay 1990).

Commercial vessels laid up pending sale and thus immobile for long period were found to be especially prone to spread the plant because their waterline is at a constant depth. Such conditions permit the development of a fringing band of *Undaria* sporophytes along the ship's hull. Ships in regular use showed very little seaweed growth on the hull. This was believed to be because their waterline is constantly changing as cargo is quickly taken on and discharged (Hay 1990).

In New Zealand a project funded by the Department of Conservation, the Fisheries Research Centre of the Ministry of Agriculture and Fisheries, and the Division of Marine and Freshwater Science, DSIR is comparing the introduced *Undaria* with the Japanese populations, monitoring its rate of spread and determining the effect on the local biota. This project is supervised by Dr Cameron Hay.



## RESULTS

### Maturation of sporophytes

Observations made on spot dives throughout 1988 on the Tasmanian *Undaria* are presented in Table 2. This infers the initiation of new sporophytes in June. These grow to maturity, reaching a peak of condition in December after which they become senescent and release spores (see Fig. 3). In March - May, there is little visible evidence of the existence of plants. Plants in Spring Bay appear to mature approximately two months earlier than the rest of the population. This agrees with the observations of Taniguichi *et al.* (1981) that *Undaria pinnatifida* plants in Japan mature earlier in embayments than on exposed coasts.

**Table 2. Chronology of *Undaria* as observed in 1988.**

When	Where	Observations
29/1/88	Rheban	Pronounced deterioration of sporophyte.
3/2/88	Rheban	"
11/2/88	Rheban	"
20/5/88	Emerald Bay-Rheban	No evidence of <i>Undaria</i> found.
16/7/88	Lachlan Is-Emerald Bay	Juveniles to 20 cm, in Johnsons Pt -Woodchip Mill area.
30/7/88	Emerald Bay	Juveniles to 20 cm, in Johnsons Pt -Woodchip Mill area.
10/8/88	Emerald Bay-Woodchip Mill	Plants to 50 cm in vicinity of Emerald Bay-Stapleton Pt, mature plants to 1.7 m in area of Woodchip Mill.
23/10/88	Emerald Bay	Plants to 1 m.
3/12/88	Emerald Bay-Johnsons Point-Woodchip Mill.	Woodchip Mill Plants deteriorating, & Emerald Bay plants mature, to 1.8 m high.
10/12/88	Maria Is-Johnsons Pt Stapleton Pt	
17/12/88	Rheban-Johnsons Pt	Emerald Bay plants showing signs of deterioration.
18/12/88	Emerald Bay-Johnsons Pt	"

### Morphological variation of the sporophyte

Plants found in shallow sheltered areas, appeared much broader, with a greater total blade area than plants found in more exposed areas (Fig.s 3 b & c). This also agrees with findings of Taniguchi *et al.* 1981, who found a similar pattern for *Undaria* in Matsushima Bay in Japan. Plants inside of the bay had greater longest pinnae and distance from base of stipe to base of incision of longest blade versus total plant length ratios than plants outside. Subsequent crossing experiments showed this variation not to be genetically determined (Kito *et al.* 1981).

Results of morphological variation in plants at Emerald Bay are shown in the graphs in Figure 4. They demonstrate that at this site maximal height occurs at 4 m depth and decreases with depth. Maximal biomass was also measured at 4 m (6 kg/m<sup>2</sup>). The density of plants increased with depth to a maximum at 8+ m. The overall form of the plants varied little with depth at this one site.

Two species of *Undaria* have been found in New Zealand, *Undaria pinnatifida* and *Undaria petersenianna* (C. Hay pers. comm.). *U. petersenianna* differs from *U. pinnatifida* in having an entire margin and does not have the distinctive convoluted sporophyll on the stipe. C Hay is maintaining a morphological monitoring program in New Zealand to explore these differences as expressed in the New Zealand plants. There was no evidence of *U. petersenianna* in this survey.

### The distribution of *Undaria pinnatifida* in Tasmania.

Location of sites from which *Undaria* has been confirmed are presented in Figure 2, indicating spread of the alga from Triabunna to at least Rheban and Lachlan Is in the South. Reports of *Undaria* at Point des Galets have not yet been confirmed. At several of the sites there was so much *Undaria* that the bottom was obscured for many square metres.

Results from transects are presented in Appendix 1. Figure 5(a) presents an idealized diagram based on the data, of the distribution of macro-algal communities in relation to exposure to wave action in the Mercury Passage. This can be compared to a similar diagram, (Fig. 5 b), constructed for the D'Entrecasteaux Channel (Sanderson and Thomas 1987). These two figures demonstrate that there is a very similar distribution of macroalgae in the two areas, the main differences being that the *Macrocystis pyrifera* of the Channel is replaced by *Undaria pinnatifida* in the Passage.

Areas with little or no macroalgal vegetation or 'bare areas' are common on rocky reef areas on sheltered subtidal coastlines of eastern Tasmania. These areas often coincide with the presence of many urchins, in particular *Heliocidaris erythrogramma*, which is believed to be the main cause of these 'bare areas' or 'urchin barrens'. *Undaria pinnatifida* was most prevalent on these former barrens. Here, cover of the ocean floor by the alga although patchy, sometimes exceeded 100%.

Cover of the *Undaria* was most obvious on the tops of boulders and in areas that did not have many refuges for the urchins. Urchins were often seen grazing on plants of *Undaria* and many plants exhibited evidence of grazers. Presumably the plant establishes itself in the spring at a faster rate than the urchins can control it. In areas where there was an abundance of native vegetation there were only isolated individuals of *Undaria*

Distribution of *Undaria* can be visualized better in Figure 6 (original results in Appendix 2.). Here the shoreline has been divided into four types, these are;

- 1    sheltered, shallow
- 2    sheltered, deep
- 3    sheltered - moderate
- 4    moderate exposure to wave action.

From this data and from the classification of the the entire infected area into shoreline types (Fig. 7) we can estimate the total amount of *Undaria* present in Tasmania. Only shores with rocky substrata are included and offshore reefs are not taken into account. Details are presented in Table 3, showing an estimated total of 411 tonnes for 1988.

**Table 3. Derivation of estimate of total amount of *Undaria* present.**

Shoreline Type	Av. Biom. at 100% cover (kg/m <sup>2</sup> )	Est. Average % cover	Length of metre strip	Est. Kg/m. of shore.	Est. length of shore type (km)	Total quantities (tonne)
1	7	30	30	63	2.6	163.8
2	3	40	80	96	0.3	28.8
3	4	30	30	36	5.2	187.2
4	7	30	30	63	0.5	31.5

**Total estimated quantity of *Undaria pinnatifida* (tonne):** 411.3

#### Culture of *Undaria* gametophytes

*Undaria*, like many other species of algae, is very fecund and this ensures successful continuation of the alga. Figures 8(a-c) show a mature sporophyll of a plant, a section of the sporophyll and individual unilocular sporangia, each containing 64 individual spores. Saito (1975) estimated that each individual plant released up to 100,000 to 1,000,000 spores per gram of the mature portion of the sporophyll per day.

Release of spores from an *Undaria* plant collected from the vicinity of the woodchip mill on the December 3, 1987 was successful. The ensuing gametophytes appeared healthy (Fig. 8 d) but sexual structures were not positively identified. A second attempt using plants collected on the December 17, 1988 from Rheban and cultured at a lower density of spore settlement, was also unsuccessful in producing obvious sexual structures in

resultant gametophytes. There was no time to follow up with more culturing attempts.

## DISCUSSION

### Effect on local biota

Introduction of foreign macroalgal species into Australian waters has been documented previously and includes *Antithamnion spirographidis*, *Polysiphonia brodiaei* and *P. pungens* (Womersley 1984). *Undaria* differs from these as it is a large, canopy forming, brown alga. Large brown algae, such as members of Laminariales and Fucales are usually ecologically dominant and keystone species in shallow hard bottom communities. Rueness (1989) writes 'Changes associated with introductions of this type of alien and the possible competitive exclusion of indigenous species may have many indirect, system-level effects on the biota'

It is difficult to determine the effect of the presence of *Undaria* on the local biota. The most likely organisms to be affected are annual macroalgae that occupy the same ecological niche. These include *Ulva* sp., *Sporochnus* sp. and various filamentous algae such as *Cladophora* sp., *Polysiphonia* sp. and *Ectocarpus* sp. These algae are small and will easily be outcompeted by *Undaria*.

In the long term there may be also a significant effect on some of the larger perennial algae. The rapid growth and canopy forming ability of the *Undaria* may hinder proper development of these longer lived algae at their juvenile phase, perhaps displacing them altogether. The most conspicuous of these perhaps is *Macrocystis pyrifera*.

*Macrocystis* used to be common in the Mercury Passage forming large beds covering large sections of the adjacent coastline (Cribb 1954). The causes of its decline during the 1970's are unknown but the more frequent

penetration of the East Australian Current in recent decades (Harris 1987, Sanderson 1987) may be to blame. The presence of the *Undaria* in the area now diminishes the likelihood of the re-establishment of *Macrocystis* even if the EAC retreats in years to come.

A similar scenario has already been reported in California for *Macrocystis* and the immigrant furoid *Sargassum muticum* (Ambrose and Nelson 1982). Following a natural disappearance of *Macrocystis* in 1976 due to elevated temperatures (El Nino), *S. muticum* invaded the available space and inhibited recruitment of *Macrocystis*.

A disturbing aspect of this study was that the *Undaria* was found to colonize all available substrates to a depth of approximately 12 m. In Japan it is recorded as growing down to depths of 15 m (Saito 1975, Akiyama and Kurogi 1982). In this study, while growth of *Undaria* appears restricted in areas of greater water movement by the more prolific growth of native algae, cover of these algae and the effect of water movement both decrease with depth. As a consequence these areas may not be restrictive to the spread of the alga as now believed.

The colonization of greater depths expands the list of algae *Undaria* is likely to compete with, the more significant being the smaller red algae. These have an optimal growing season in the spring coincident with *Undaria*. As the *Undaria* can shade out the smaller algae, and its growth rates are comparatively quick, it has the capacity to out-compete these plants for light. The red algae are a very prominent part of the deeper subtidal flora. The result of such a disturbance is presently unknown and as the subtidal macroalgal flora in Tasmania is so little understood (there still remain many undescribed species), long term differences in the flora may never be fully appreciated.

Effects may be more evident in other areas, however, such as further up the food chain. Red algae for example are known to be a preferred food of

the abalone and probably serve as a breeding ground for many invertebrates that form the diet of various fish species.

Also many *Undaria* plants were seen being consumed by urchins. Will this increase population numbers of urchins so that when the alga disappears in late summer, the urchins will then turn to the more established algae?

Introduction of foreign seaweeds to the coastlines of other countries has proved detrimental. For example the alga *Sargassum muticum* has been introduced from Japan to both European and North American coastlines where it has proliferated and choked waterways and become hazardous to shipping (eg. Jones and Farnham 1973, Norton 1976, Critchley *et al.* 1983, Rueness 1989). Much has been consequently spent on eradication programs.

In Australia, as long as there is little or no control on the likely means of introduction *ie.* via ballast waters, there is a risk of contamination of our waters by not only seaweeds, but by a variety of potentially harmful organisms. Introductions actually traced to ballast waters to date, include the toxic dinoflagellate *Gymnodinium catenatum*. Ballast waters have been shown as the potential vector of marine organisms ranging from species of fish to amphipods, crabs and shrimps.

#### Potential spread within Australia

Factors influencing the distribution of macroalgae on a local scale (kms) include water motion, substrate type, salinity and nutrient availability but on an oceanic scale temperature has long been recognized as the prime factor (Setchell 1915). Van den Hoek (1982) inferred with some degree of success, phytogeographic boundaries of a number of species of benthic algae from experimentally determined critical temperatures limiting essential events in their life histories. For a temperate species, boundaries used were

similar to those stressed by Hutchins (1947) for marine benthic animals. These are for the southern hemisphere:-

- 1 The 'northern lethal boundary'. This corresponds to the highest summer temperature a species can survive during a period of 2-4 weeks.
- 2 The 'northern growth boundary'. This corresponds to the highest winter temperature which over a period of several months permits growth.
- 3 The 'northern reproductive boundary'. This corresponds to the highest winter temperature which over a period of several months permits reproduction.

4, 5 and 6 corresponding southern boundaries.

Table 4 details maximum and minimum temperature tolerances and optima obtained from literature for gametophytic and sporophytic generations of *Undaria pinnatifida*. Using this information we can extrapolate as to the likely potential distribution for *Undaria pinnatifida* within Australia.

**Table 4. Temperature tolerances for the sporophyte and gametophyte generations of *Undaria pinnatifida*. (From Akiyama 1965, Akiyama and Kurogi 1982, Arasaki and Arasaki 1983, Saito 1975 and Zhang *et al.* 1984.)**

	Sporophyte	Gametophyte
Lethal temperatures	<0°C, >25°C	<-1°C, >30°C
Growth boundaries	<3.5°C, >20°C	<10°C, >24°C
Reproductive boundaries	<7°C, >23°C	<10°C, >24°C



Thus, while sea water temperatures at Macquarie Is. (1466 km southeast of Hobart, 4-7°C, Loewe 1957) will permit growth of the sporophyte, temperatures are too low for reproduction of either the gametophyte or sporophyte stages. Northern boundaries corresponding to February isotherms ((maximal summer temperatures, from Rochford 1984, see Fig. 9) that would affect these critical life stages are presented in Table 5. The limiting factor north of the present distribution would appear to be the time required for growth of the sporophyte to maturity. This assumes that the sporophyte is able to grow to maturity at temperatures between 15°C and 20°C within six months .

The February 22°C isotherm corresponds to Cape Leeuwin in the SW of Australia and Wollongong in the east (see Fig. 10). The alga thus has the potential to colonize a very significant portion of the coast of Australia.

**Table 5. Northern isotherms limiting essential life events in the life history of *Undaria pinnatifida*.**

	Sporophyte	Gametophyte
Northern Lethal isotherm	23°C	28°C
Northern Growth Boundary	22°C	26°C
Northern Reproductive Boundary	25°C	26°C

Isotherms limiting distribution in Japan are the 0°C winter isotherm in the north and 27°C summer isotherm in the south (Funahashi 1974). The greater apparent distribution in Japan is due to the large temperature fluctuation between summer and winter of coastal waters enabling longer periods at temperatures conducive to growth of the sporophyte.

Bardach *et al.* (1982) recorded *Undaria* as growing in waters of salinity ranging from 27 to 33 ppm. This would preclude *Undaria* from occupying estuaries.

The finding by Hay (1990) of plants growing on the hulls of New Zealand fishing boats and the capacity for the plant to attach to a variety of substrates also indicates the potential for a fast invasion.

#### Introduction of *Undaria pinnatifida*

Three likely avenues for the introduction of *Undaria* to Tasmanian waters are;

- 1) Japanese tuna fishing boats
- 2) Introduction with intentionally introduced mariculture organisms
- 3) in the ballast waters of cargo boats transporting woodchips from Tasmania to Japan.

Japanese longline tuna boats do not frequent this area and introduction from mariculture operations is unlikely as there are no recorded introductions of cultured organisms to Tasmania from possible source areas and present quarantine procedures would preclude this event.

Information in regard to the direction of currents in the Mercury Passage suggest a predominantly southerly direction (Tasmanian Department of Sea Fisheries pers. comm.) and the present distribution of *Undaria* is consistent with an initiation of infection in the Triabunna region. Ships that pick up woodchips for Japan dock at Triabunna prior to taking on cargo, discharge ballast waters in quantities which may exceed 25,000 tonnes and can include sediment from the bottom of the holds. Cargo ships have been proven as a potential vector for the introduction of species of fish, amphipods, crabs and shrimps to Australia (Williams *et al.* 1988). Foreign organisms believed to have been introduced by this means include the toxic dinoflagellate *Gymnodinium catenatum* (Hallegraef *et al.* 1988) and the 'aggressive alien' mussel *Musculista senhousia* (Willan 1987). Introduction via ballast waters of cargo ships would appear to be the most

likely vector for the introduction of *Undaria pinnatifida* to Tasmanian waters.

In Japan, *Undaria pinnatifida* is the third largest maricultural plant crop after *Porphyra* and *Laminaria* (Michanek 1975). It is also used for feed in the mariculture of juvenile abalone (*Haliotis*, Tamura 1970). Interest has been expressed in utilizing the local Tasmanian *Undaria pinnatifida* for both these purposes. However, this requires the local State Fisheries Authority to address the implications of encouraging dispersal of this foreign organism. The introduction of large quantities of this plant to the coastline will not be without some longer term effects and an assessment of the likely impact of this species is required. Eradication of this alga is out of the question due to the elusive, microscopic gametophytic stage of the alga and the extent of colonization.

## SUMMARY

*Undaria* is a brown alga exhibiting an alternation of generations. These are a macroscopic sporophyte and a microscopic gametophyte. It is an annual plant, the sporophyte appearing in late winter, maturing in summer and releasing spores in late summer as the plant deteriorates. Little evidence can be found of the plant from late autumn to mid winter. Timing of these events can vary to some degree (1-2 months) depending on situation.

*Undaria* presently inhabits the shoreline from Triabunna to Rheban in the south with isolated plants found at Lachlan Is and there are as yet unsubstantiated reports of plants at Point des Galet.

*Undaria* has the capacity to attach to a variety of substrates, can tolerate a wide extreme of exposure to wave action and was found inhabiting the shore from Mean Low Water down to the extent of available

substrate in the infected area of Mercury Passage (12 m), indicating a wide potential area of colonization.

*Undaria* is a very prolific plant with biomass levels now in the Mercury Passage of up to 10 kg/m<sup>2</sup>, individual plants up to 1.8 m high and with densities of up to 100 plants/m<sup>2</sup>.

Individual mature plants have the capacity to release millions of spores each day.

*Undaria* has been found to attach to the hulls of boats and been able to withstand periods of cruising without becoming detached, indicating the possibility of rapid spread to new areas.

Due to this high fecundity, the elusive gametophyte and the present extent of distribution, eradication of the plant would be expensive, difficult and probably impossible.

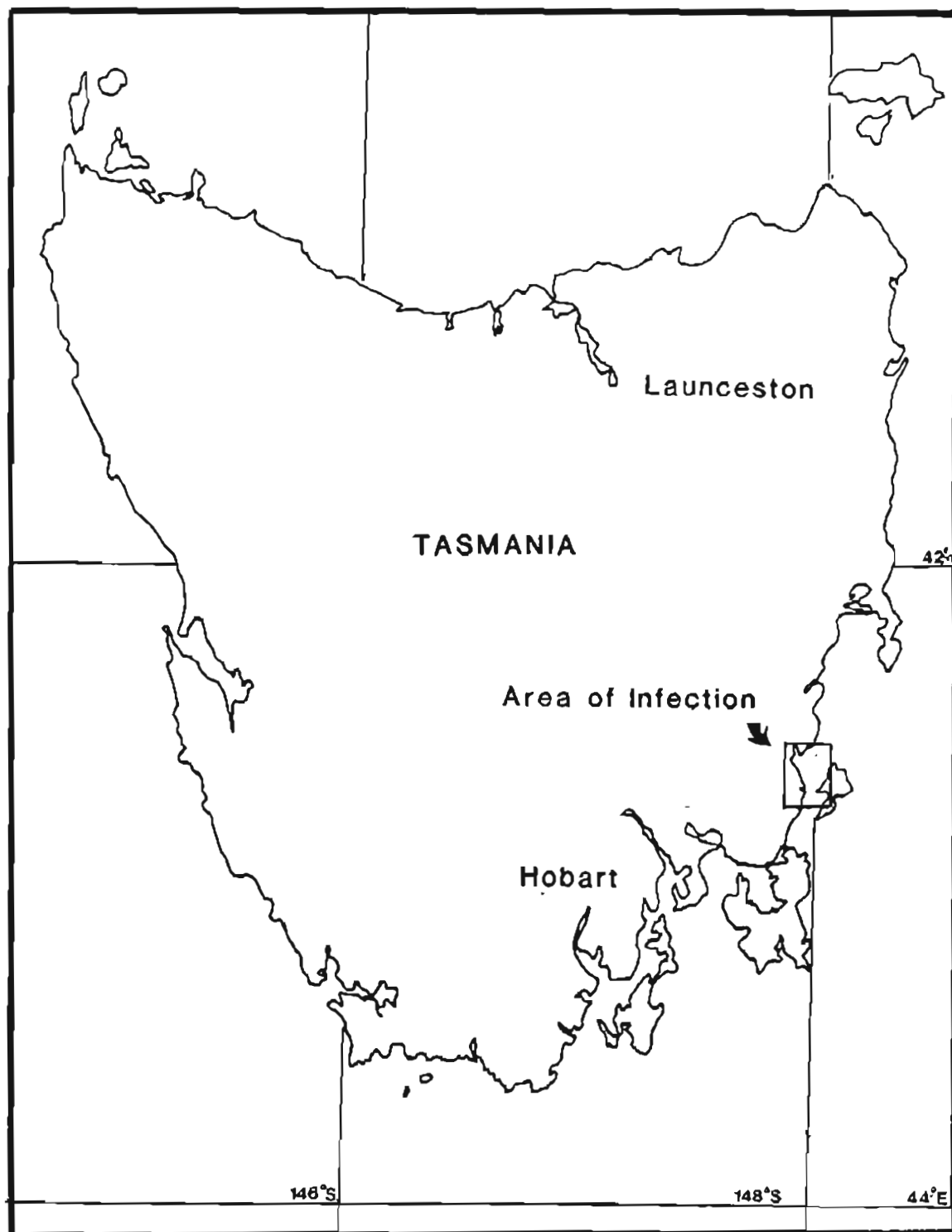
Evidence suggests a possible colonization of the shore on Australian coasts from Cape Leeuwin in south west Western Australia to Wollongong on the New South Wales Coast.

Effects on the local biota are difficult to determine. One potentially threatened alga is 'String Kelp' or *Macrocystis pyrifera*. This alga occupies a similar ecological niche and may be out-competed by the *Undaria*.

*Undaria* has also been found in New Zealand and France. Programs have been established in both areas to monitor effects of its introduction on the local biotas.

Evidence suggests ballast waters from the cargo ships that transport woodchips to Japan as the most likely means of introduction. This demonstrates a need for legislation to effect controls on ballast waters to prevent further introductions of potentially deleterious organisms.

Fig. 1 Map of Tasmania showing study area and region of infection of *Undaria pinnatifida* within Tasmania.



**Figure 2.** The position of transects, 'drop dives' and the presence or absence on *Undaria* within the study area.

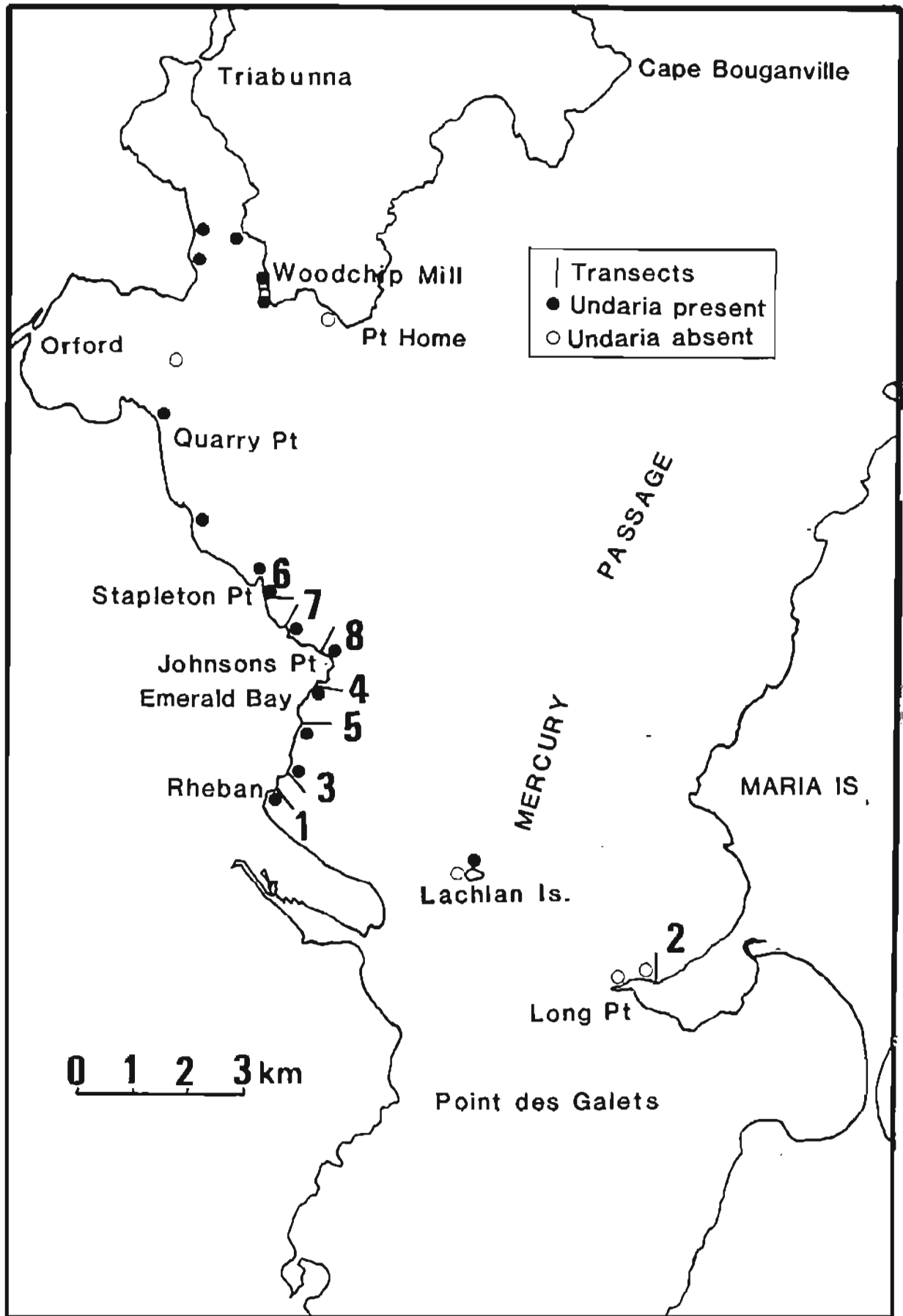


Figure 3. (a) juvenile *Undaria*, (b) mature morphotype exposed to wave action, (c) mature morphotype from a sheltered environment, (d) senescing plant.

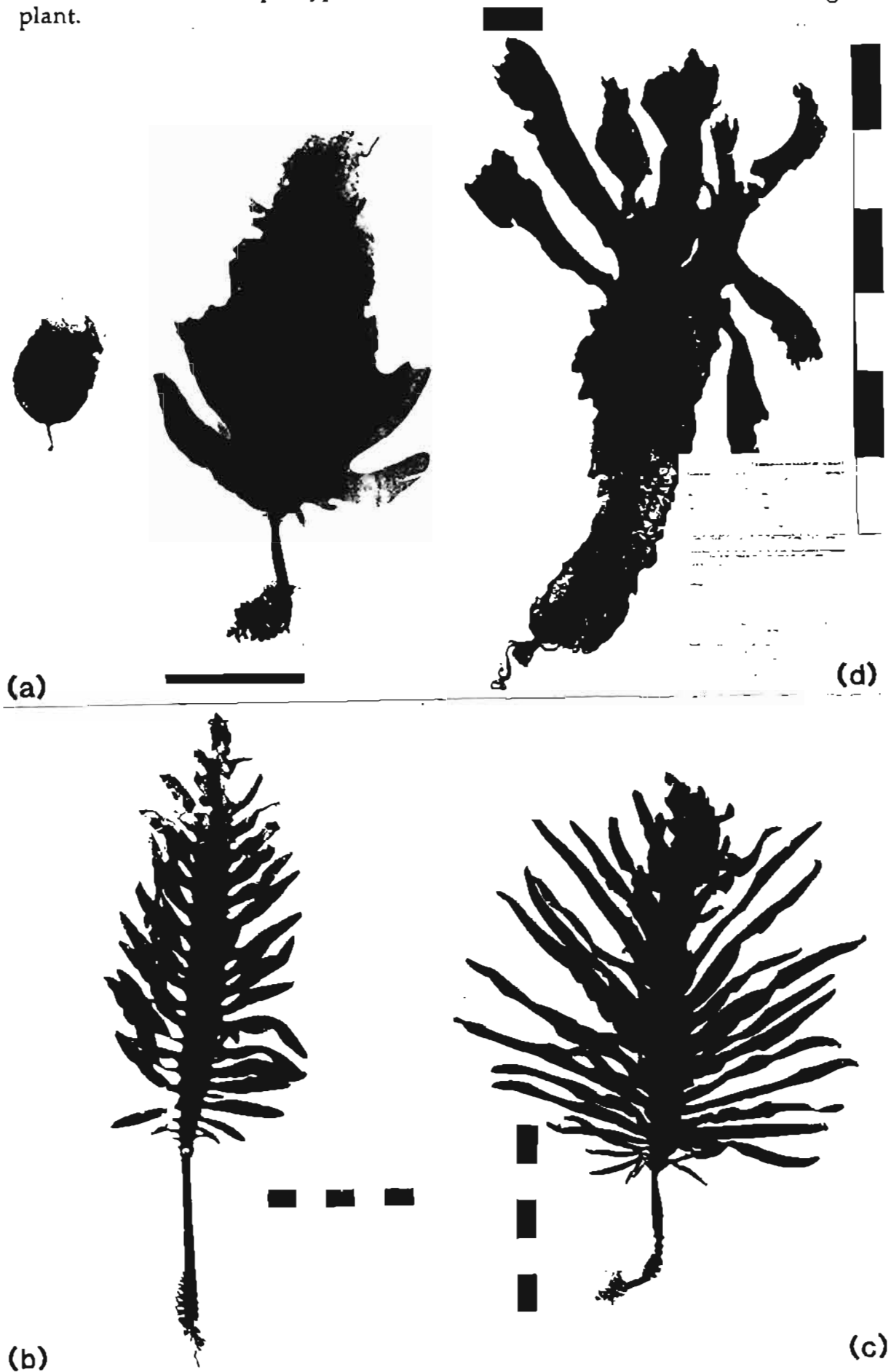
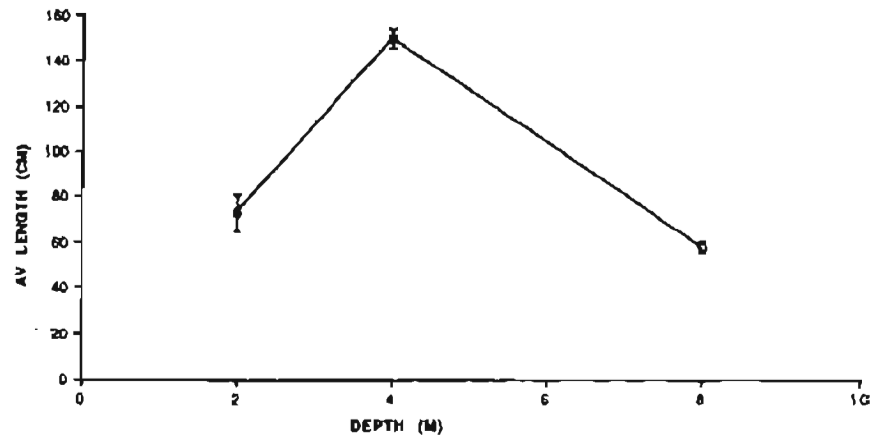
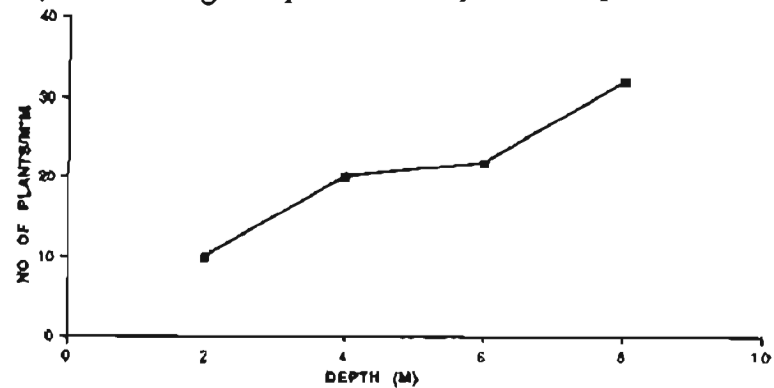


Figure 4. Details of morphometric analysis from plants collected at Emerald Bay (3/12/88).

(a) Change in average length of *Undaria* plants with depth.



(b) Change in plant density with depth



(c) Change in average plant weight with depth.

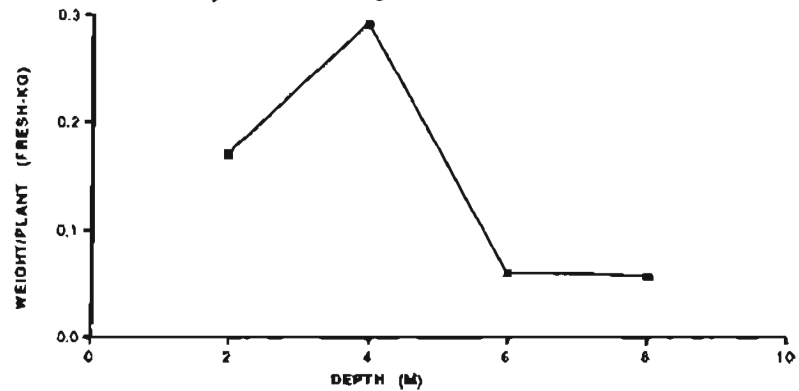
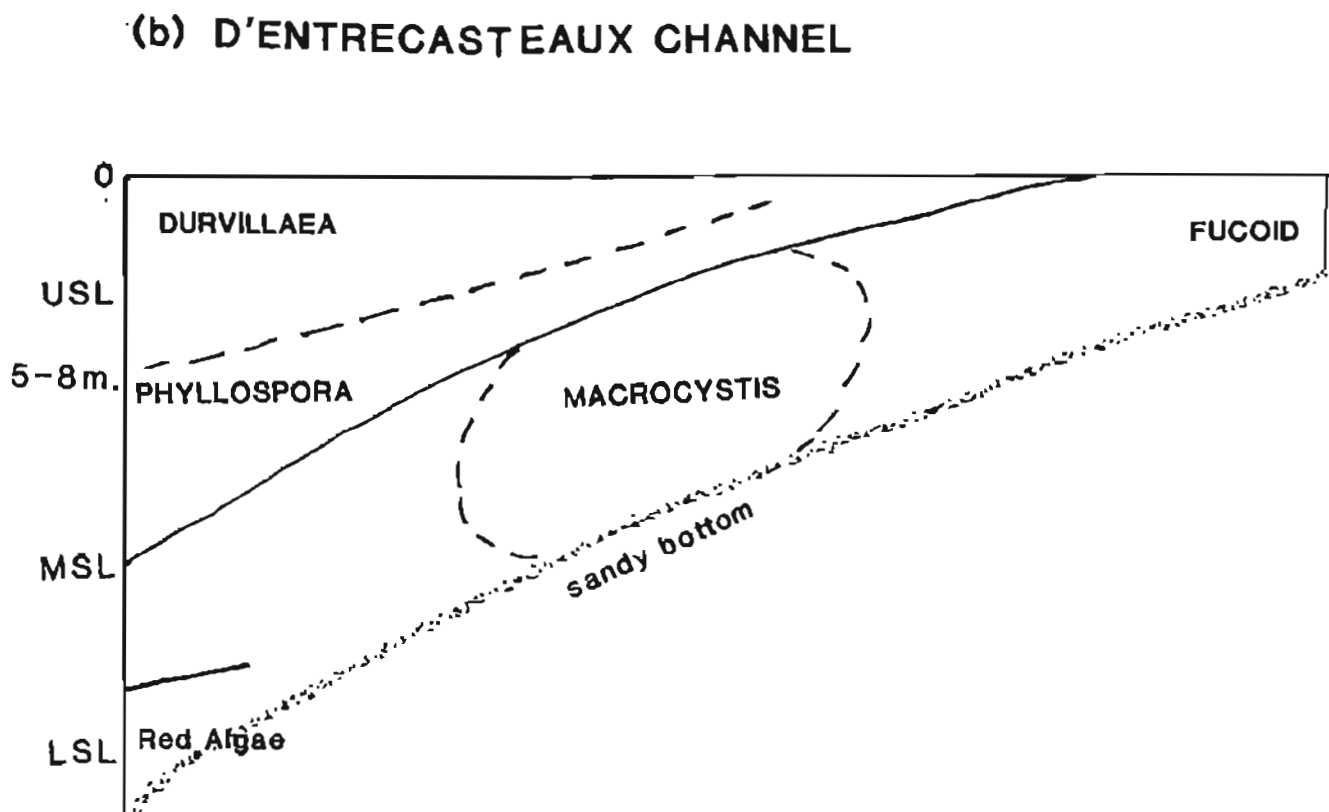
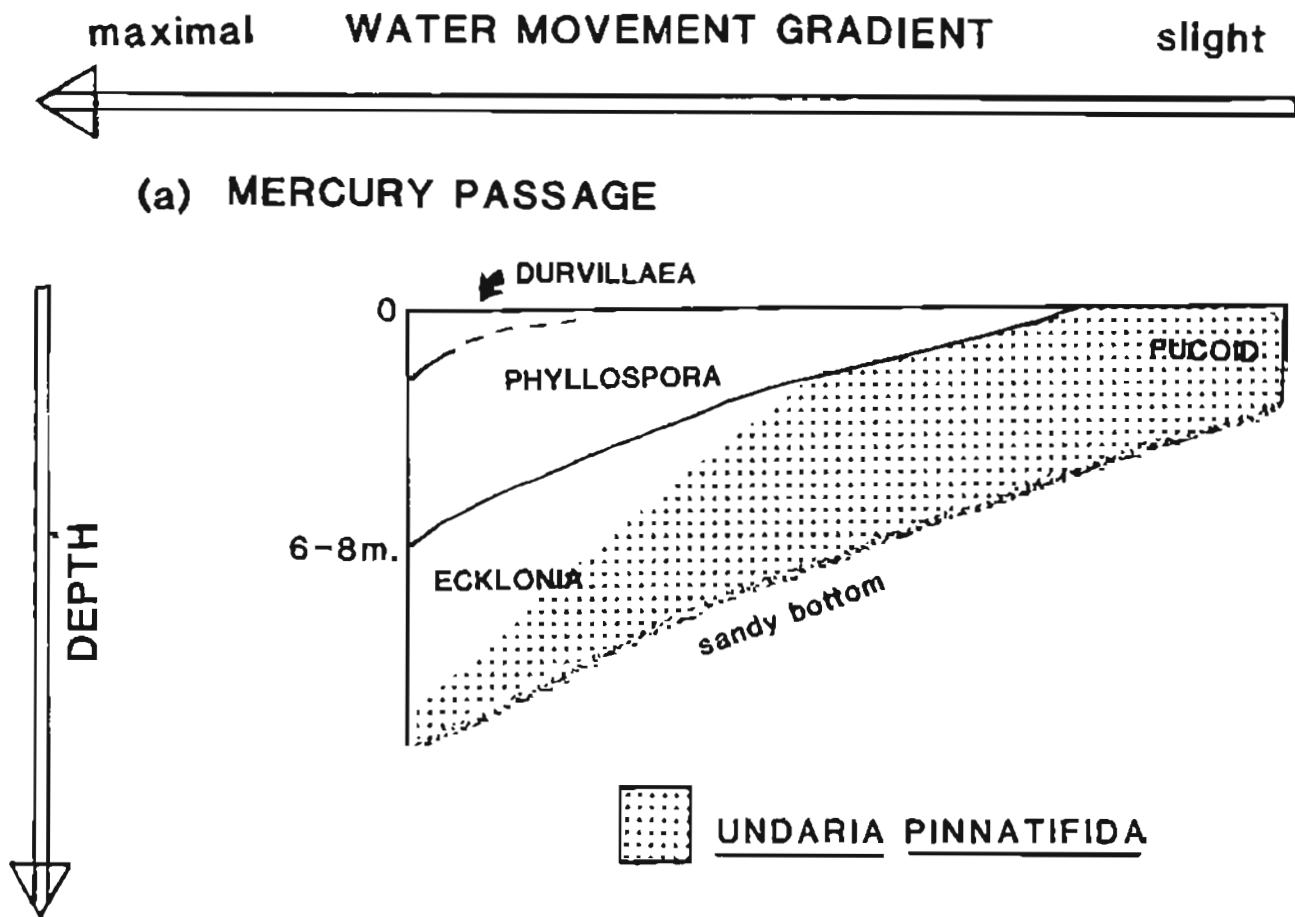
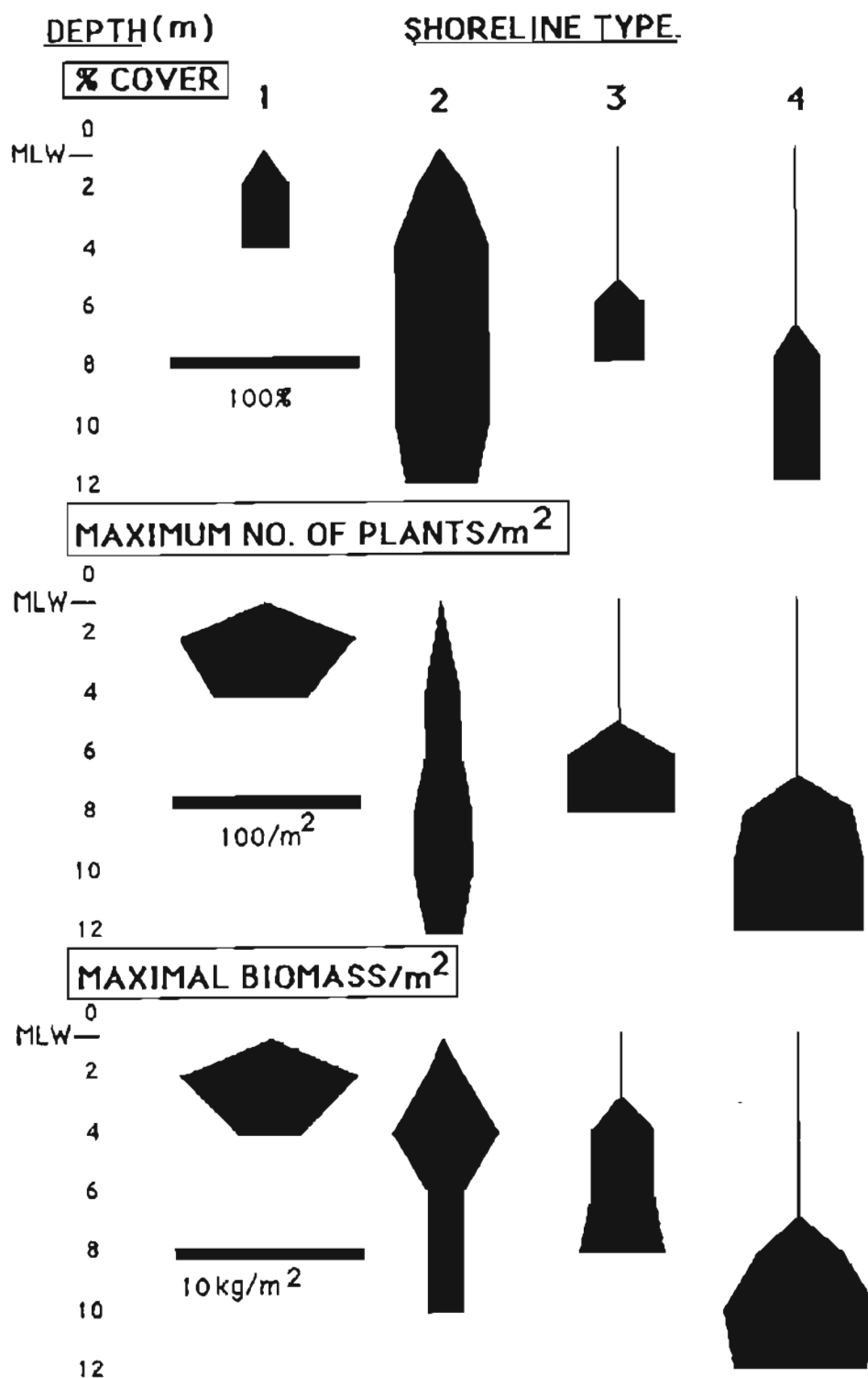




Figure 5. Diagram showing the change in macroalgal distributions with depth and exposure to wave action in (a) the Mercury Passage and, (b) the D'Entrecasteaux Channel (from Sanderson and Thomas, 1987).





**Figure 6.** Diagram showing determined distribution of *Undaria pinnatifida* in the Mercury Passage by depth for four different shoreline types; 1. - sheltered, shallow, 2. - sheltered, deep, 3. - sheltered, moderate and 4. - moderate, exposure to wave action (note - lower limit of *Undaria* distribution set by lack of substrate resulting in the abrupt finish in distribution for each of the shoreline types ie. 4, 12, 8, & 12 m depth for the four shoreline types respectively.)

**Figure 7.** Classification of the shoreline infected by *Undaria pinnatifida* into the four types.

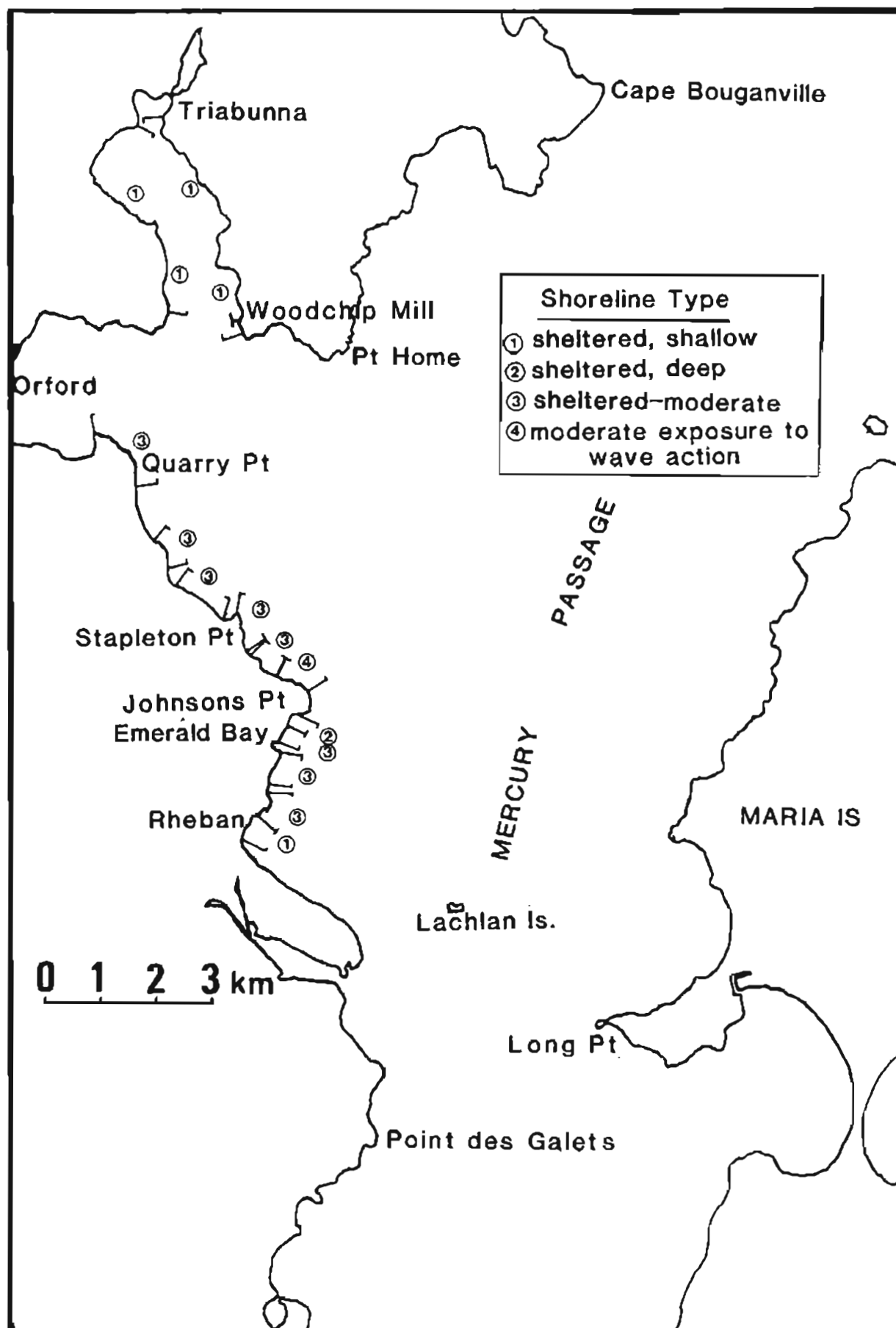


Figure 8. (a) sporophyll of a mature plant, (b) section of sporophyll surface showing spore sacs, (c) individual spore sacs, (d) gametophyte at approximately 2 weeks.

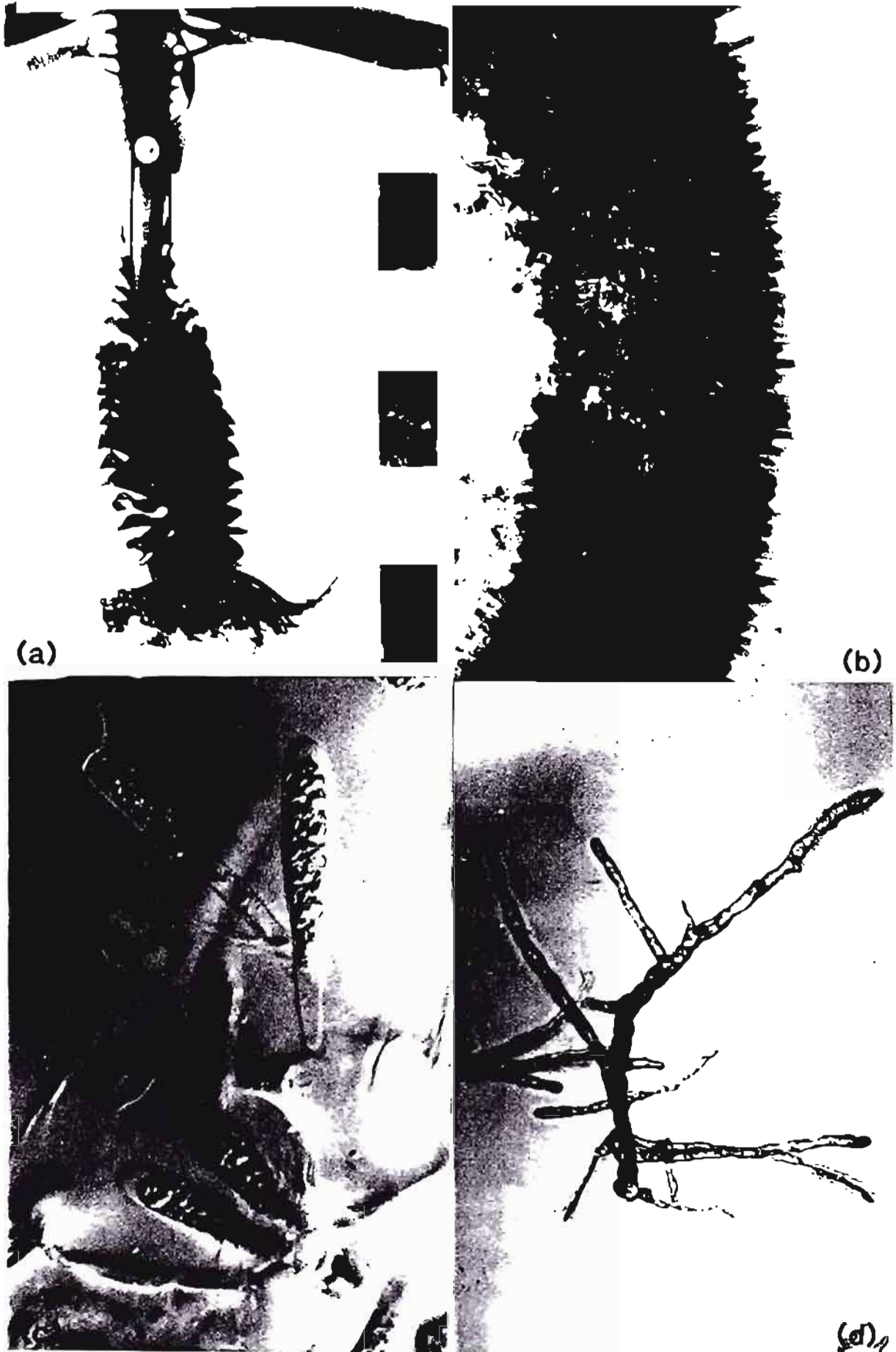


Figure 9 (a-d). Temperature of surface water (solid lines) and air temperature (dashes) at the limits of *Undaria* distribution in Japan. (a) and (b) northern limit, (c) and (d) southern limit. (Funahashi 1974).

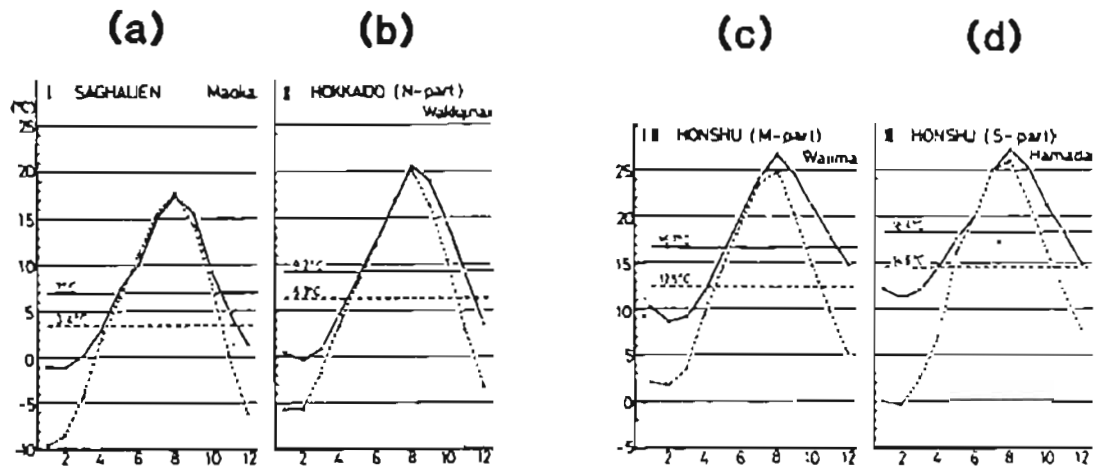


Figure 9 (e-f). Temperature of surface waters in Tasmania. 'The Jams' - NW Tasmania; Adelaide Bay - NE Tasmania (Thompson et al. 1982). Triabunna - study site; George III Reef - SE Tasmania (DSF and Sanderson-this thesis).

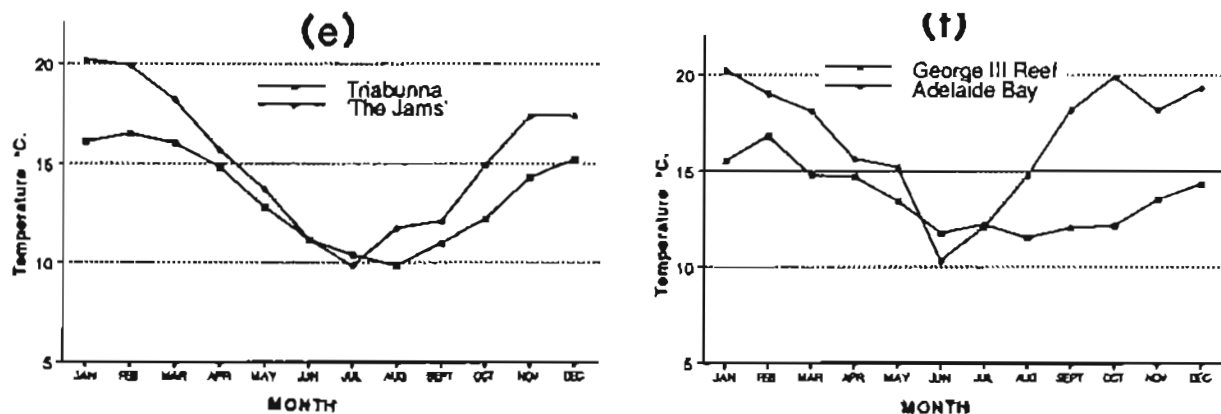
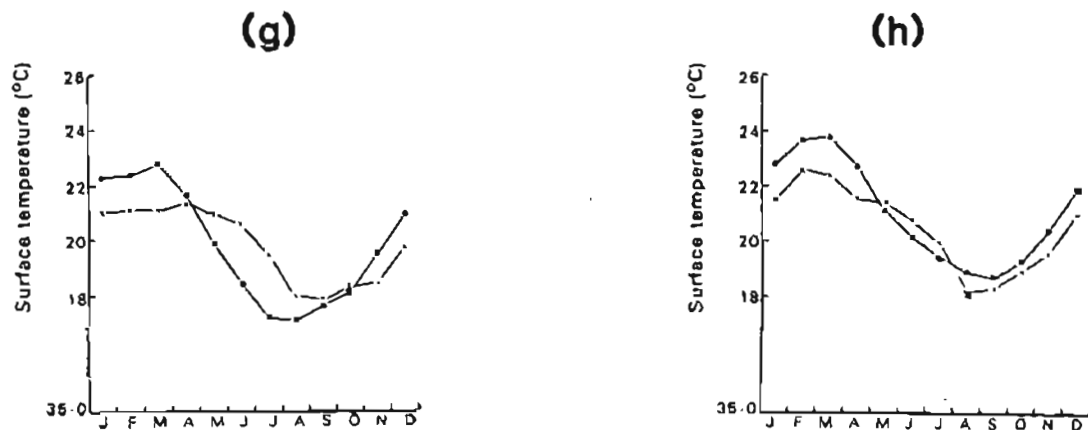
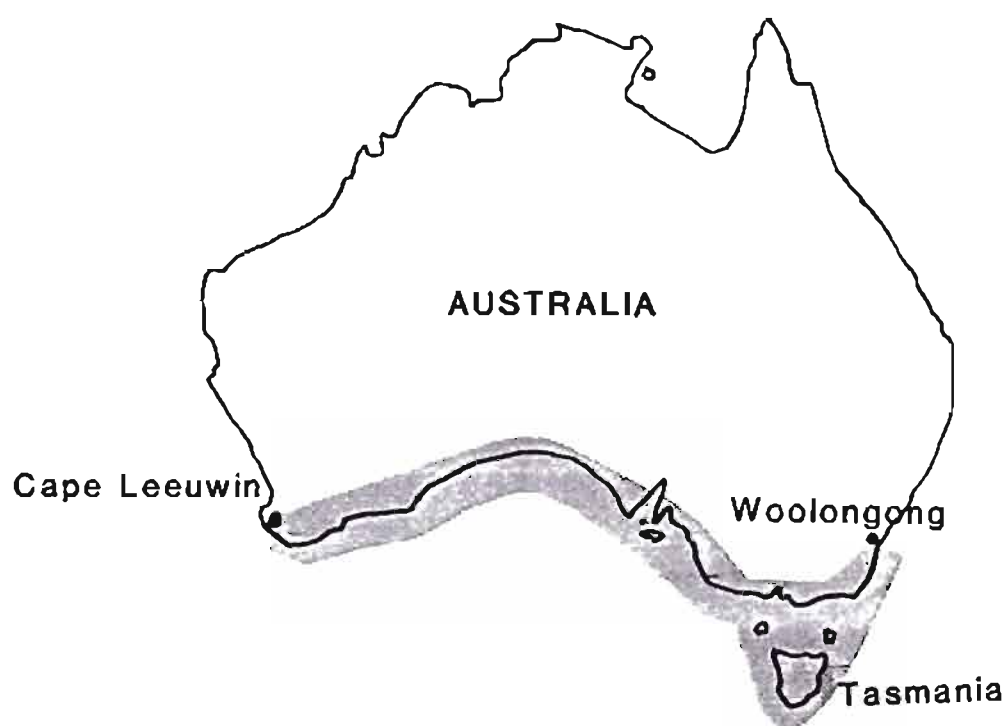


Figure 9 (g) Water temperature at the locality of the February 22°C isotherms on Australia's west coast (Cape Leeuwin) - x, east coast (Woollongong) - •. (h) Water temperatures at sites 10°N of those sites in the preceding figure.



**Figure 10.** Potential area of infection by *Undaria pinnatifida* in Australian waters (stipled).



## **PART 2**

### **Growth of Macroalgae at Two Sites on the East and South- Eastern Coasts of Tasmania.**

## PART 2, CHAPTER 1.

### INTRODUCTION

This study was initiated to investigate the seasonality, and major abiotic factors affecting the productivity of dominant subtidal macroalgal species in Tasmanian coastal waters. Information thus acquired may aid in the interpretation of differing degrees of success in catching animal species in various parts of the state especially those dependent on macroalgae for food, such as the abalone *Haliotis rubra* Leach, and the sea urchin *Heliocidaris erythrogramma* Valenciennes. The ultimate goal of this study was to improve the management of these fisheries.

#### Ecology of Kelp Communities

There are many studies relating to growth strategies and community dynamics of macroalgae but most have been centred principally in the northern hemisphere e.g. in California (Neushul and Harger 1987, Dayton *et al.* 1984, Zimmerman and Kremer 1984, Gerard 1982 a, b, c and Foster 1975) on *Macrocystis pyrifera*; in Nova Scotia, Canada (Gagné *et al.* 1982, Chapman and Craigie 1977 and Mann 1972 a, b), on *Laminaria* spp.; in Vancouver, Canada (Druehl 1978 and Pace 1972) on *Macrocystis integrifolia* and in the eastern Atlantic (John 1971 and Kain 1963, 1964) also on *Laminaria* spp. Of the few studies conducted in the southern hemisphere, most concern either *Ecklonia radiata*, e.g. Larkum (1986) and Kirkman (1981) in Australia and Novaczek (1984 a, b) in New Zealand, or *Macrocystis pyrifera* (Tussenbroek 1989 a, b, c, Santileces and Ojeda 1984 a, b) in South America. The available literature is vast and diverse. Some of the more comprehensive reviews include those of Kain (1989), Chapman (1986),



Schiel and Foster (1986), Dayton (1985), Lobban *et al.* (1985), Mann (1982), Lobban and Wynne (1981) and Kain (1979).

This thesis is concerned with the abiotic rather than the biotic factors that affect plant growth as these are more likely to be affecting the productivity of the community as a whole. Important abiotic factors influencing kelp communities include light, nature of substrate, sedimentation, nutrients, water motion, salinity and temperature (e.g. Chapman 1986, Lobban *et al.* 1985, Dayton 1985, Lobban and Wynne 1981). In this study, rocky coastlines with offshore reefs exposed to the open ocean and distant from freshwater outlets were selected as study sites. This is the typical coastal environment for much of the west, south and east coasts of Tasmania. The factors most likely to be affecting the growth of algae along these shores are light, temperature, nutrients and water motion. Factors such as sedimentation and freshwater inflows can largely be ignored.

### Light

Light may be considered to be the most important physical factor affecting plants. It has been shown that macroalgae adapt to a variety of light climates by varying the total and relative amounts of pigments (Ramus 1981). However, the quality and quantity of irradiance are critical to all stages of algal life-histories. Marine plants have pigments that absorb light in the waveband of 350-700 nm. Saturation of photosynthesis is exhibited in intertidal seaweeds at quantum irradiances of 400-600  $\mu\text{mol m}^{-2}\text{s}^{-1}$ , in upper and medium sublittoral species at 150-220  $\mu\text{mol m}^{-2}\text{s}^{-1}$  and deep water red algae at 60-70  $\mu\text{mol m}^{-2}\text{s}^{-1}$  (Lüning 1981). Compensation irradiances for photosynthesis vary from 5-25  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . Analogous levels for growth can vary from these values by a factor of ten, lower for saturating and higher for compensation irradiances. Saturating irradiances for growth of young and microscopic stages are 1/5 to 1/8 of corresponding

adult plants. Values of minimum growth requirements for gametophytes of some Laminariales are as low as  $0.2 \mu\text{mol m}^{-2}\text{s}^{-1}$ . The amount and quality of light at any given site can be determined by the depth, the presence of canopy plants and/or the turbidity or colour of the water.

Photoperiodic reactions have only been recognized in macroalgae only relatively recently. Triggers have been demonstrated for reproductive cycles, growth and control of life histories.

### Temperature

After light, temperature is considered the most important physical factor in the environment of plants because of its affects on molecular activities and properties, and hence on virtually all aspects of metabolism. Biochemical rates approximately double for every  $10^{\circ}\text{C}$  rise in temperature, although enzyme reactions reach an upper temperature limit above which changes in tertiary or quaternary structures inactivate and ultimately denature the enzymes (Lobban *et al.* 1985). Photosynthesis, respiration and growth, being sequences of enzyme reactions, also have optimum temperatures, but the effects of temperature are not uniform across all processes. These optima vary between and within species.

Surprisingly little is known about the relationship between temperature and the growth processes of kelp (Dayton 1985), partly because the inter-relationships with other factors are complex and it is almost impossible to isolate temperature effects from many other environmental effects in the field. For example, light compensation and saturation points are closely dependent upon ambient temperature (Lüning 1980), as are nutrient absorption and growth. 'Warm water die offs' of southern Californian kelps were long thought to be caused by higher temperatures in certain years but they now appear to result from nutrient depletion because  $\text{NO}_3^-$  concentrations in coastal waters are inversely related to temperature

(Zimmerman and Kremer 1984). Kelps can survive high temperatures in the presence of adequate nutrients (Jackson 1983, 1984).

Kain (1989) stresses the importance of temperature as a 'trigger'. For example, the survival of several red algae near their northern limit in Nova Scotia has been shown to be dependent on summer temperatures high enough for growth to be fast enough for them to be competitive (Novaczek *et al.* 1987). Temperature influences reproductive condition, and in regions of extreme temperature change, some seaweeds have life history events cued by temperature.

Through the effects on life history and the temperature range tolerances of seaweeds, temperature affects the geographic distribution of seaweeds and is probably the principle large-scale regulatory factor; salinity, wave action, and substratum play important but local roles in phytogeography.

### Nutrients

The importance of nutrients to the growth of algae is well recognized, particularly in the case of nitrate, though phosphate and other trace compounds may also be important (De Boer 1981). The seasonality of nutrient stress is well known but the effects are confounded by other factors, especially temperature. Apparent storage of nutrients has been observed for *Laminaria* (Gerard and Mann 1979, Gagné *et al.* 1982, Chapman and Craigie 1977) and *Macrocystis* (Gerard 1982 a, b, c, Wheeler and North 1981), and experimental fertilization of kelp forests with nitrate have improved growth (Chapman and Craigie 1978, Dean and Jacobsen 1984).

### Water Motion

Types of water motion vary from currents and internal waves to surge and surface waves, and each can affect macroalgae at the individual

and the community level. Water motion at the algal surface has been shown to aid in nutrient exchange (Wheeler 1980), while surge is often important determinant of plant mortality (Seymour *et al.* 1989, Dayton *et al.* 1984) and thus the productivity of a community (Gerard 1976, Santileces 1977). Many species exhibit morphological plasticity in response to water motion (Norton *et al.* 1981) and this can affect productivity levels. In a study on *Laminaria longicruris* Gerard and Mann (1979) postulated that the lower productivity level of an exposed coast population was the result of adaptation to high intensity water movement. Water motion can affect light availability by moving canopies and influences the impact of sedimentation and scour. In South Africa wave-induced sweeping of the fronds of *Laminaria pallida* maintains bare space and excludes herbivores (Velimirov and Griffiths 1979) and in California wave stress influences community structures (Dayton *et al.* 1984).

#### Tasmanian Phycological Studies

The poor state of knowledge of the ecology and physiology of subtidal macroalgae in Australia results from a dearth of investigators. The majority of studies that have been done worldwide are in areas where commercial utilization of seaweeds occurs. In California, *Macrocystis* has been harvested either for potash or alginates since before the first world war. In Canada, there is a large industry based on carrageenans principally from *Chondrus crispus*, and in Europe there are a number of alginate-based industries (Chapman and Chapman 1980). In Australia there is little utilization of seaweeds for industrial or other purposes (Sanderson and Di Benedetto 1988).

An initial survey and study of *Macrocystis* in Tasmania by Cribb (1954 b) resulted in the establishment of a harvesting and processing operation in Triabunna on Tasmania's east coast. However, this closed in the early

seventies due to financial and technical difficulties, exacerbated by low yields (Sanderson 1987a).

The only significant macroalgal based business is conducted on King Is., off the north west tip of Tasmania. Here, drift *Durvillaea potatorum* is collected from the shore, dried, pulverized and shipped to Scotland where it is used in alginate production.

Two abalone rearing ventures on Tasmania's east coast use quantities of seaweed for feed. The larger of these, based in Swansea, was using as much as a tonne a week during peak growth periods (1991).

Interest in Tasmanian seaweeds dates back to early discovery voyages of D'Entrecasteaux (1791-4), Baudin (1802), Flinders (1801-3), D'Urville (1837-40) and Sir James Ross (1839-43) with JD Hooker as botanist (Ducker 1981). Many type specimens for southern Australia were collected from Tasmanian shores. In the early 19th century several naturalists devoted time to seaweeds including Ronald Gunn, Rev. J. Fereday, Dr Jeannerette, William Archer and Mrs Loisa Meredith. They sent collections on to eminent phycologists such as Hooker, Harvey and Mueller in Europe. Between 1853 and 1856 Harvey visited Australia and made extensive collections including Tasmania and with Hooker published 'Flora Tasmaniae' (Hooker 1860) making the Tasmanian algae probably the best known of Australian algae at that time (Womersley 1959). However, the latter half of the 19th century was a quiet period for phycology in Tasmania.

Significant collections made in the early half of the twentieth century include those of Levring, Mrs Florence Perrin, and Lucas and Rodway with Lucas (1928) publishing a list of Tasmanian algae (Edyvane Unpubl. Hons Thesis 1981). In the 1950's Eric Guiler, a zoologist, made descriptive studies of the intertidal ecology, including the vegetation. Guiler also published a list of Tasmanian algae (Guiler 1952), bringing the work of Lucas up to date. Most of Guiler's identifications were made by A. B. Cribb. Cribb published a

species list for Port Arthur (Cribb 1954a) and new records for the state (Cribb 1956). Since then, collections have been made by a number of 'mainland' - Australian phycologists, e.g. H.B.S. Womersley and K. Harada.

More recently, studies have been initiated on the ecology of the subtidal macroalgae. G. Edgar, also a zoologist, has described the general zonation of subtidal marine organisms including macroalgae around Tasmania (Edgar 1981, 1984) and conducted work concerning the the meiofauna associated with macroalgae (Edgar 1983 a, b, c, d, 1984a, b & 1987). In 1987, Sanderson and Thomas described the macroalgal distribution and factors affecting that distribution in the D'Entrecasteaux Channel. Department of Sea Fisheries Technical Reports have also ensued including a report concerning the state of the *Macrocystis* stocks in Tasmania (Sanderson 1987a), this study (Sanderson 1987b), the potential for an industry based on edible seaweeds in Tasmania (Sanderson and Di Benedetto 1988, Sanderson 1988) and publications concerning the introduction of the Japanese seaweed *Undaria pinnatifida* to Tasmanian waters (Sanderson and Barrett 1989, Sanderson 1990).

### The Study Sites

Tasmanian coastal waters have been found to be predominantly subantarctic or subtropical water masses (Harris *et al.* 1987), with the subtropical convergence being the boundary between them. The position of this boundary varies seasonally and from year to year. The coastline of the south eastern and western sides of Tasmania are washed predominantly by the cooler and comparatively nutrient enriched sub-antarctic current, while the east coast is affected more by warmer subtropical waters and is subject also to incursions of the East Australian Current (EAC). This current occurs sporadically in late summer and rarely passes south of Maria Island. It is a warm water current originating in the Coral Sea off Queensland. Apart

from localized inputs, significant effects due to freshwater discharge are believed to be confined to the D'Entrecasteaux Channel and the west coast (Clementson *et al.* 1989). The waters of southern and eastern Tasmanian coasts respectively would thus appear to be quite different and without the complication of significant freshwater input. Therefore they may be expected to support different productivity levels. Site selection was based on these premises and accessibility.

The initial program was to establish a means of monitoring the growth of a number of species of macroalgae at George III Reef, then to apply these techniques to the same species at a second site, Bicheno. Growth parameters were correlated with measured environmental factors to reveal principal controlling agents.

Species selection was influenced by consideration of principal macroalgal species by biomass in Tasmanian coastal waters. The species chosen were *Durvillaea potatorum* (Bull Kelp), *Phyllospora comosa* (Cray Weed), *Macrocystis pyrifera* (String Kelp) and *Ecklonia radiata*. At George III Reef, the red algae were a prominent part of the flora and were also monitored. The study of *Durvillaea* was later abandoned due to the plant's habitat in the surge zone, and the subsequent difficulties of researching this alga.

From a consideration of the literature, nitrate limitation of plant growth was anticipated. Proof of this occurring was sought by monitoring levels in plant tissues and in seawater during the initial program. This aspect was dropped however because later technical complications prevented investigation of this question. Any associations of growth of the plants with nitrate concentrations in the seawater are thus limited to circumstantial evidence.

## SUMMARY

The aim of the project was to compare the growth of selected species of macroalgae at two sites in the hope of obtaining an indication of the principal factors affecting the productivity of the macroalgae around Tasmania. This was to be extrapolated to help interpret variation in commercial yields of animal species from different areas of the coast, in particular, those animals directly dependent on macroalgae for food, such as the abalone *Haliotis rubra* and the sea urchin *Heliocidaris erythrogramma*. This in turn was expected to help improve management of these fisheries.

Many studies have been done concerning the growth of macroalgae in the northern hemisphere, but few in the south and as a consequence most of the literature concerns northern hemisphere species.

Few studies have been conducted in Australia on the biology of subtidal macroalgae and even fewer in Tasmania.



## PART 2, CHAPTER 2.

### THE COASTAL ENVIRONMENT

#### INTRODUCTION

Study sites were selected so as to maximise possible differences in oceanic water types whilst maintaining similar factors of exposure to wave action, substrate and distance from freshwater outlets. The sites also had to be readily accessible from Hobart. The two sites chosen were George III Reef (south east coast of Tasmania) and Bicheno (central east coast of Tasmania).

George III Reef (see Figs 2.1 and 2.2) was chosen as it was already the site of an on-going study into abalone conducted by the Tasmanian Department of Sea Fisheries (DSF). This meant there could be some joint work, reducing the resources required. The site had been chosen by the DSF because they considered that it was most representative of coastal waters along the south and west coasts of Tasmania while still within reasonable commuting distance of Hobart. The south and west coasts are influenced by subantarctic waters for much of the year, evidenced by cooler sea-water temperatures, higher salinities and nutrient concentrations, relative to the eastern and northern Tasmanian coastal waters (Rochford 1975 b, Harris *et al.* 1987, Clementson *et al.* 1989 and Harris *et al.* 1991).

Bicheno (see Figs 2.1 and 2.3) was chosen as the contrasting site. The coast here is mostly subject to the influence of warmer subtropical waters. The East Australian Current (EAC) is recorded as coming as far south as Bicheno in most summers rarely passing further south than Maria Is. (Harris *et al.* 1987). The EAC originates in the Coral Sea off the Queensland

coast and is characterized by higher temperatures and salinities and low nutrient concentrations compared to Tasmanian coastal waters generally.

The aim of this section was to first define the two sites including community descriptions, then to characterize the hydrological and physical parameters for correlation with later growth studies. The macroalgal community composition is contrasted with analogous communities studied elsewhere outside of Australia.

## METHOD

### Site Details

#### George III Reef

To facilitate the abalone work, a 0.5 km long transect line consisting of one centimetre thick cable anchored with steel train wheels and concrete was laid down across the reef. Initially this was marked with small buoyed lines every 5 m and proved to be a convenient reference point for relocation of sampling sites (providing one could find the transect line!). Sampling sites were adjacent to a section of this line, equivalent to the stated distance from datum or '0'. Datum point was in deeper water (14 m depth) where a second line crossed at right angles (see Fig. 2.4).

In December 1984 a metre square quadrat, subdivided into twenty five 20 x 20 cm squares, was used to facilitate a description of the macroalgal community at George III Reef. The cover of algal species was recorded at 10 m intervals adjacent to the transect line. Each alga was given a percentage cover reading based on the number of squares occupied. A metre square quadrat was used as this size has been used in other studies relating to macroalgal community analysis and it was large enough to allow representative readings of all relevant species.

Data was recorded on waterproof surveying film. Identification of many of the red algae proved difficult underwater and these were listed simply as 'fleshy red algae' except for *Plocamium dilatatum*, the most abundant red alga at the site.

Total cover for a given quadrat may exceed 100% due to the combined contributions of three and sometimes four strata of algae.

With the exception of *Macrocystis pyrifera*, major species quantities remained so throughout the period of the study. The quantities of *Macrocystis pyrifera* were not expected to change significantly during the study and thus no on-going monitoring of the overall state of this alga was conducted.

#### Bicheno

The site at Bicheno was originally chosen for the apparently healthy stands of *Macrocystis pyrifera* with *Ecklonia radiata* and *Phyllospora comosa* all in close proximity. Triangulation with objects on the shore was used to find the site at each visit. A descriptive survey of the benthic vegetation was conducted in January 1989 for comparison with the George III Reef site. This was undertaken using 200 m of measuring tape as a transect line running out perpendicular to the shore. Again a metre square quadrat, subdivided into twenty five 20 x 20 cm smaller squares, was used as a measure of the percentage cover of algal species at 5 m intervals, adjacent to the transect line. These were recorded on surveying film along with bottom type, depth and other general observations. As at George III Reef the algae that were prominent at the start of the study remained so throughout the study.

#### Measurement of Hydrological Parameters

In conjunction with the regular sampling in relation to growth of plants, measurements of hydrological parameters were taken on site on a

regular basis to confirm the differences between the two sites and for later correlation with growth. This included regular sampling of the sea-water for analysis at the CSIRO Hobart Marine Laboratories for salinity, 'nitrates' (nitrates and nitrites), silicate and phosphate and on-site measurements of temperature and light attenuation.

### Sea-water sampling

For the first year of sampling at George III Reef, nutrients were sampled with a Niskin bottle at 0.7 m and 14 m at the deep site (0) and at 2 m over the Reef. Samples were frozen as soon as possible on return to the laboratory and stored frozen until analysed. Analyses of nutrients were determined using a Tecator 5023 flow-injection analyser with a Tecator 5023 spectrophotometer and a Hewlett Packard 7123A chart recorder (see Clementson *et al.* 1989). Separate samples were taken for salinity. These were stored in airtight polyethylene bottles until analysed. Salinity was measured by the methods of Major *et al.* (1972).

The result demonstrated that the water was well mixed over the Reef (Sanderson 1987b). As a consequence it was decided that only one sample plus a duplicate was necessary. This was taken from 1 m depth over the deep site.

At Bicheno, water samples were taken at 1 m depth at a point where there was at least 12 m depth of water in close proximity to the site.

### Light attenuation

Light attenuation was measured with a LI-COR, LI-192 S underwater quantum sensor combined with a LI-185 meter. This measures quanta in the range 400-700 nm, the photosynthetically active range (PAR) in accordance with guide-lines set down by UNESCO (Kirk 1977). Light was measured regularly at the surface, at 1 m, 2 m, 5 m, 10 m and 15 m depths. Attenuation

was determined from the relationship describing the attenuation of light through water:

$$I_z = I_0 e^{-kz}$$

where  $I_z$  and  $I_0$  are the downward quantum irradiances (flux of quanta per unit area on a horizontal surface) in the photosynthetic waveband at depth  $z$  and 0 m respectively and  $k$  is the vertical attenuation coefficient for PAR (Kirk 1977). Light determinations were conducted outside the *Macrocystis pyrifera* kelp forests. Occasional readings were done inside the forest for comparative purposes.

### Temperature

At most sampling sessions, temperature near the surface was measured at both sites with a -10 to 50° C mercury thermometer.

### CSIRO and Bureau of Meteorology Data

#### Temperature and Nutrients

The distance of George III Reef and Bichenō from Hobart, the vagaries of the weather and the high cost on time and money of visiting these two sites meant that measurements of hydrological parameters on-site could not be done on a regular basis. CSIRO Marine Laboratories, Hobart, maintain long term monitoring sites close to the two sampling areas. These are at Storm Bay (close to George III Reef) for temperature, salinity, nitrate and phosphate data and off Maria Island (close to Bichenō) for temperature, salinity, nitrate but no phosphate data. These two sites also were not influenced by near shore coastal irregularities such as from coastal benthic communities or from creek or river discharges and thus were representative of prevailing oceanic conditions. While these records are not

a perfect measure of conditions at at both the sites they do appear to reflect the broad features of weekly, seasonal and interannual variability.

The results from Storm Bay (every two weeks, 1985-1988) were used in the regression analysis at George III Reef as they are taken on a more regular basis than the on - site sampling regime. CSIRO samples were taken at ten metre depth intervals from 0 to 50 m. Sets of results for the different factors at each of the depths were correlated against the same factors measured on site (Storm Bay and George III Reef only). This showed the most appropriate set of results for use in regression analyses.

Measurement of sunshine, Total Global Radiation and sea state were obtained courtesy of the Bureau of Meteorology. The closest stations to the sample sites for these observations are at Bicheno and Grove (for George III Reef) for daily light readings and at Eddystone Lighthouse (for Bicheno) and Bruny Island (for George III Reef) for sea state. Figures for Total Global Radiation were available only from Hobart Airport which lies midway between the two sites.

#### Hours of sunshine

Sunlight was recorded at the Grove and Bicheno weather stations on sunshine recorders. These operate by measurement of lines burnt in rotating cards. This standardizes sunshine measurement from station to station. Average daily readings obtained from the Bureau of Meteorology, were used for regression against determined growth rates.

#### 'Total Global Radiation'

This is total solar irradiance, incident and diffuse, in wavelengths from 300-3000 nm. The units of measurement are megajoules/m<sup>2</sup>. A conversion factor of:

$$1 \text{ MJ m}^{-2} = 4.2 \text{ mol m}^{-2} \text{ year}^{-1}$$

was obtained from Lüning (1981). There is no general agreement as to what proportion of total radiation received constitutes photosynthetically active radiation (PAR). This component tends to vary with the optical properties of the air mass being, 38-45% with a clear sky or 48-69% with cloud cover (Wood 1987 b).

### Water Motion

The quantification of wave action, especially at the level of the plants is notoriously difficult (e.g. Doty 1971, Lobban *et al.* 1985, Russell and Fielding 1981) and usually some subjective measure is employed. In the absence of a better method, estimates of sea state based on recorded observations at light houses near to the study sites were utilized.

The state of the sea is estimated by standard methods at each of the lighthouses. Swell (regular waves of distant origin), direction and size, as well as sea state (waves of irregular size and direction created by local winds) are recorded every hour throughout daylight hours.

Eddystone Lighthouse is the closest lighthouse to the Bicheno site (see Fig. 2.1). While ninety five kilometres separates Eddystone and Bicheno, the two sites have a similar aspect, and differences in seastate experienced are expected to be minimal. This assumption is supported by a long term analysis of sea and swell state observations at Bicheno and Eddystone conducted between 1960 and 1980 (Underwood 1987). While he recognized the likely existence of error due to the subjective nature of the readings, very similar overall mean sea and swell states for the two areas were demonstrated.

Observations from Bruny Island Lighthouse are used for George III Reef. While Bruny Island Lighthouse is close to George III Reef (see Fig. 2.2) conditions may be expected to differ due to differing aspects and the influence of an extensive reef system, 0-20 m deep, but mostly 10-20 m deep,

extending from south-west of George III Reef to the east-south-east, including Actaeon Island, Sterile Island and Black Reef. This would have the affect of abating conditions, mainly those due to swell from the south west and south. For this reason correction factors were introduced to the Bruny Island Lighthouse recordings. They were calculated from the angle of the incident wave direction relative to that direction which is fully open to swell at George III Reef. Swells from an easterly direction are experienced in full at the Reef and no correction was applied. Swells from the south were multiplied by 0.75, swells from the south-west by 0.5 and confused swells by 0.5. While these correction factors have not been proven they would seem the best option given available information and calculated swell states agreed well with those observed. Construction of a more exact relationship would not be possible without much extensive experimentation and analyses (J Reid, Oceanographer, CSIRO pers com.).

### Statistics

Correlations are computed as the product moment coefficient, 'r' otherwise known as 'Pearson's' correlation coefficient. This coefficient is a measure of the degree of linear relationship between variables. Fisher's table relating significance levels to the correlation coefficient were used for 'p' values. 'r<sup>2</sup>' is the 'coefficient of determination' and is the proportion of the total variation in 'y' that is explained or accounted for by the fitted linear relationship (Snedecor and Cochran 1980). Statistical tests were conducted using either Statview or Systat, two software packages that run on 'Macintosh' microcomputers. All stated or depicted errors are standard error.



## RESULTS

### Site Descriptions and algal flora

#### George III Reef, physical characteristics.

George III Reef (43° 31'S, 146° 58'E) lies approximately six kilometres south of Southport and two kilometres out to sea (Fig. 2.2). It is a dolerite reef out-cropping from sand in 12-16 m of water. The shallowest part of the reef is one metre from the surface at mean low tide. The upper portions of the reef, < 6 m deep, consist of an irregularly surfaced dolerite mass with many fissures and outcrops. At depths of 6-9 m below the more turbulent upper waters are large boulders and a more dissected bottom. From 9 m to the edge of the reef in 15 m of water, the slope is not as great and the incidence of sand increases, the majority of the bottom consisting of solid reef with occasional higher outcrops and large rocks. At 15 m on the northern side, the bottom is predominantly sand with outcropping reef. The distances from the 9 m contour to the edge of the reef on the more wave exposed southern and eastern sides are much shorter (~150 m) than on the less exposed northern side (~300-400 m).

The Reef is named after a vessel of the same name wrecked on the reef in 1834 with the loss of 134 lives. Little evidence can now be found of the wreck as it has been destroyed by years of pounding seas.

The Reef and surrounding area is on record as being the source of prodigious amounts of abalone (*Haliotis rubra*), and hence the interest from the Tasmanian Department of Sea Fisheries. However, it has since been discovered that abalone divers have claimed this area for their catches, because it is the southern most legal limit of their boating licenses when in fact, they ventured further south. The area, nonetheless, still produces large amounts of abalone. Also in evidence are large numbers of *Jasus novaehollandiae* Holthius, the southern rock lobster.

## Macroalgae of George III Reef

The results for the transect conducted in December 1984 are presented in Figs 2.5-2.6. The macroalgal vegetation is typical of an exposed shoreline in this area (Sanderson and Thomas 1987), with three distinctive communities;

1. From 1.5-6 m depth there is a belt dominated by *Durvillaea potatorum*. The abrasive action of the fronds of the massive *Durvillaea* plants allows few other erect foliose algae to survive. Subcanopy plants include some of the hardier red algae such as *Erythrymenia minuta* and *Callophyllis* spp. Occasional plants of the brown algae *Macrocystis pyrifera*, *Cystophora platylobium*, *Sargassum paradoxum*, *Xiphophora gladiata* and *Phyllospora comosa* and the green algae *Cladophora* sp. and *Bryopsis* sp. also occur in this zone. The majority of the rock surface is covered extensively between the *Durvillaea* holdfasts by encrusting corallines.

2. A distinctive band of *Phyllospora comosa* surrounding the reef between the 6-8 m depth contours. The species composition of understorey plants of this zone is intermediate in character to the zones above and below it.

3. Immediately below this zone is the beginning of a zone which extends from 8 to 15 m depth. It is dominated by red algae, the most abundant species being *Plocamium dilatatum*, a branched plant 20-30 cm high. It spreads adventitiously by rhizomes. Also very common is *Sonderopelta coriacea*, a prostrate alga having the appearance of aggregations of red plates 15-20 cms in diameter. *Caulerpa flexilis*, a green alga, appears seasonally. It too spreads adventitiously by rhizomes and presumably 'overwinters' in this form. In spring, it grows rapidly to 30 cm in height and blankets patches metres in diameter. From 8 m depth down to

15 m however, the overall dominant alga is *Plocamium dilatatum*, with over 75% cover for much of the area.

The dominance of red algae at this depth contrasts with other areas in south eastern Tasmanian coastal waters under similar conditions where the dominant algae are the larger canopy browns such as *Phyllospora comosa*, *Ecklonia radiata* or *Macrocystis pyrifera*. In this zone at George III Reef, *Ecklonia* and *Macrocystis*, although present, do not maintain substantial areas of continuing occupation.

In water from 8-12 m depth the most abundant of the tall canopy-forming plants is *Macrocystis pyrifera*, the areal densities of the fronds varying greatly. When this project was initiated in late 1984, *Macrocystis* formed a canopy of moderate density around the entire reef. By late 1987, however, this had virtually disappeared with only isolated plants remaining. At the time of writing (mid-late 1989), the *Macrocystis* had returned to about half the initial densities. When abundant, many plants can be found to the reef edge in 15 m of water, but the highest densities are in depths of 8-12 m.

In deeper water, 12+ m, *Ecklonia radiata* is the most abundant brown alga. Distribution is patchy however, in contrast to many areas of surrounding coastline where *Ecklonia* can often obscure most of the bottom. At these depths at George III Reef there is much sand due to the proximity of the reef edge. This, the competition with the dominant red algae (sensu Shepherd 1980) for space, and the low levels of light may contribute to the lack of *Ecklonia*. *Ecklonia* appears more prevalent in other areas of relatively 'clean' reef bottom and clearer waters. The sandy bottom is more suitable for the rhizomatous spread of some of the red algae including *Plocamium* spp. and the green alga, *Caulerpa flexilis* (see Appendix 3 for full species complement at George III Reef).

Bicheno, physical characteristics.

Amongst Tasmanian recreational SCUBA divers, Bicheno is best known for its clear, deep waters. The site selected is at Cape Lodi (148° 19'S, 41° 54'E), away from the activities of the many SCUBA divers that frequent the area. It is approximately 230 m from shore in 11 m of water. Rock type is granite. This formed a solid reef from above the shoreline to depths greater than 25 m. The surface is dissected by gullies and the occasional boulders. Patches of sand are more prevalent at depths below 11-12 m. The majority of the reef surface is featureless, sloping away from shore providing little protection for macroalgae in a heavy swell. At depths greater than 13 m the bottom is more irregular giving more protective niches for seaweed.

#### Macroalgae at Bicheno

A transect conducted in January, 1989 (see Figs 2.7 and 2.8) shows the distribution of algae down to approximately 13 m depth. Algal cover in this zone tended to be patchy. Below this depth, cover of *Ecklonia radiata* was continuous with some *Macrocystis pyrifera*. Again the cover of *M. pyrifera* proved to be very variable. The site was initially selected in early 1987 on the basis of the presence of large quantities of *M. pyrifera*. A visit in May of 1988, revealed virtually all the weed had disappeared except in deeper waters (>14m). Presently (mid-1989) the alga is returning to the area, and levels are approaching original.

As at George III Reef, despite the patchiness, the vegetation at Bicheno may be divided into three main communities, depending on the depth;

1. *Durvillaea potatorum* zone from 0-2 m depth.
2. *Phyllospora comosa* zone extending from 2-10 m depth and an
3. *Ecklonia radiata* zone below 10 m, the upper 3 m of which is distinguished by patches of *Phyllospora comosa*.

The presence of sand on the relatively flat reef surface and wave action results in wave induced scouring. The algal flora in scoured areas throughout the depth range (to 12 m depth) is characterized by *Cystophora xiphocarpa*. In the low intertidal areas it is confined mainly to protective gullies. The alga occurs in conjunction with turf forming algae in the shallower waters (down to 6 m), while in deeper waters it occurs in association with *Halopteris* sp. and *Sporochnus* sp. The algae present in scoured areas have a varying resistance to scour, with an apparent gradient radiating out from sand traps on the reef surface. *Halopteris* appears the most resistant and is present closest to the sand, it is followed by *Cystophora xiphocarpa*, *Sporochnus*, *Ecklonia* and then the least resistant, *Phyllospora*.

*Macrocystis pyrifera* was conspicuous below 2 m depth at the time of the descriptive survey in January 1989. During the period early 1988 to mid 1989 when *Macrocystis* was rare, isolated plants were always present in the deeper waters (>14 m). In shallower waters at this time, there existed occasional smaller, spindly plants. This may have been the second species of *Macrocystis*, *M. angustifolia*. This may form an intergrade with *M. pyrifera*, but this was not investigated further. Womersley (1987) has recognized plants with intermediate characters as occurring in this area of Tasmania.

Other algae included articulated Corallines and fleshy red algae such as *Plocamium dilatatum*. The red algae may have formed a further zone deeper than the *Ecklonia radiata* belt (> 18 m) but this was not confirmed.

Encrusting Corallines were common throughout the depth range. Their presence may have been encouraged by the sand on the reef. These algae are known to withstand periods of cover (Miles and Meslow 1990).

### Herbivores

The plants once established, at both the sites rarely if ever had evidence of grazing by herbivores and it was believed to be a negligible

factor in growth of the plants studied. At Bicheno there were large numbers of the 'turban shell' or 'periwinkle', *Turbo undulata* (Lightfoot, 1786) and the 'seaweed shell', *Phasionotrochus eximius* (Perry, 1811). Many of these were found on the plants but no evidence was found of damage due to grazing. When the *Macrocystis* disappeared in early 1988, many of these shells that had been on the *Macrocystis* were then found on the *Ecklonia* and the *Phyllospora*. Examination of the fronds showed scraping marks on the surface of the fronds from the radulas but no tissue damage. Perhaps they were feeding on exudates or epiphytes. Due to the large densities of these shellfish (often  $> 10\text{-}15/\text{m}^2$ ), some levering effect was quite likely on the macroalgal community present most likely through feeding of the microscopic stages of the algae on the reef surface.

#### On Site Measurements of Temperature and Salinity

Water temperatures at George III Reef (Fig 2.9 a) for the period 1985-88 demonstrate a clear seasonality with a minimum of  $11.0\text{-}12.5^{\circ}\text{C}$  in June-August and maximum of  $15.5\text{-}17.1^{\circ}\text{C}$  in December-February. The limited data for Bicheno (Fig. 2.9 b) suggests a similar periodicity but with a minimum of  $12^{\circ}\text{C}$  in July and a maximum of  $19^{\circ}\text{C}$  in February. Change in salinities with time at both places, however is not as obviously seasonal and there is not a direct relationship between salinity and temperature. In general, salinities are lower with lower temperatures and vice-versa. Relatively high temperatures and salinities were experienced in early 1988 at both sites under the influence of the East Australian Current. This current was experienced from March to May at both sites, followed by a warm winter and thus for this particular year, differences between the sites were minimal.

### On Site Measurements of Nutrients

The change in nitrate concentration at both sites is seasonal (Fig. 2.10 a and 2.10 b). At George III Reef from 1985-6, relatively high nitrate concentrations are maintained from May-November. In 1987-8, however, the concentration of nitrate peaked in May-July and decreased from then on. Change in nitrate concentration at Bicheno was similar for this period, except for two extraordinary peaks, one in August 1987 of  $8.5 \mu\text{M NO}_3$  and the second in December 1988 of  $10.5 \mu\text{M NO}_3$ . The validity of these must be doubted however and they may have resulted from contamination of samples. Average nitrate concentrations at George III Reef for the four year period are  $2.4 \mu\text{M NO}_3$  ( $2.4 \mu\text{M NO}_3$  for 1987-8) and at Bicheno;  $2.5 \mu\text{M NO}_3$  for 1987-8 (not including the two spurious high readings). Phosphates ( $0.43 \mu\text{M PO}_4$  average at George III Reef and  $0.36 \mu\text{M PO}_4$  at Bicheno) and silicates ( $1.095 \mu\text{M SiO}_2$  at George III Reef and  $1.09 \mu\text{M SiO}_2$  at Bicheno) generally did not vary greatly at either site.

### Correlation with CSIRO Storm Bay and Maria Island Data

Figures 2.11-2.12 show temperature, salinity, nitrate and phosphate for Storm Bay and Maria Is. Table 2.1 (page 70) shows the results of correlation analysis at George III Reef and in Storm Bay. They all show closest association with waters from 20 m in Storm Bay. Temperature and salinity are highly correlated with  $r$  values of 0.926 and 0.84 ( $p < .001$ ) and indicate similar water masses at both sites. Results from 20m in Storm Bay are thus best for further regression with plant growth parameters at George III Reef. Waters from 20m depth in Storm Bay are likely to correlate best with the water at 1-10 metres depth at George III Reef due to the mixing of waters in the upper few metres of the water column at inshore coastal sites. Nitrate and phosphate concentrations are more likely to suffer as a result of sampling technique and high spatial variability and the lower correlation

values of 0.552 and 0.491 ( $p < .01$ ) are not necessarily an indication of real differences between the two sites. Storm Bay is considered to give a better picture of the broader scale variation occurring due mostly to the more regular, frequent sampling regime.

### Sunshine

Average daily sunshine recordings for the sampling period are presented in Fig. 2.13. On an annual basis, Bicheno would appear to be slightly sunnier by nearly an hour per day with an average of 5.88 hours/day compared with 5.12 hours/day at Grove. Both stations demonstrated an occasional reduction in November-December. This corresponds to high wind and overcast weather common at this time of the year in Tasmania.

### Transmittance

Table 2.2 gives the results of LICOR quantum meter readings taken at George III Reef and Bicheno for the period of the study. They have not taken as regularly as might have been desired due to service difficulties with the LICOR. They do however demonstrate that waters at Bicheno were consistently clearer than at George III Reef with euphotic depths half again as great as that at George III Reef. This agrees with personal observation. The Bicheno site is adjacent to deeper water, granite reefs and there are few freshwater inputs in the area. The water is thus clearer and suspended sediment is generally larger in size and falls out of the water column quickly. At George III Reef, there are many shallow reefs, some continually exposed to swells, maintaining a higher load of sediment in the water column by constant stirring. Readings taken in the kelp forest on three occasions at George III Reef at different times demonstrate a 25% decrease, on average, of available light at 10 m depth compared to outside.



**TABLE 2.2.** Coefficient of extinction (Average  $\pm$  s.e.), and consequent calculated euphotic depths (depth of 1% surface irradiance) at (a) George III Reef and (b) Bicheno.

**(a) GEORGE III REEF.**

<b>DATE</b>	<b>Extinction Coefficient k (ln)</b>	<b>r<sup>2</sup></b>	<b>p</b>	<b>Depth of 1 % surface irradiance (m)</b>
10/4/87	0.219	0.946	0.001	21.0
16/4/87	0.207	0.950	0.0009	22.2
3/7/87	0.264	0.878	0.006	17.4
29/10/87	0.161	0.969	0.001	28.6
5/7/88	0.172	0.934	0.002	26.7
26/1/89	0.137	0.935	0.002	33.6
<b>AVERAGE</b>	<b>0.193</b>	<b>(<math>\pm</math> 0.019)</b>		<b>24.9</b>

**(b). BICHENO**

<b>DATE</b>	<b>Extinction Coefficient k</b>	<b>r<sup>2</sup></b>	<b>p</b>	<b>Depth of 1 % surface irradiance (m)</b>
21/4/87	0.165	0.903	0.004	27.9
22/4/87	0.135	0.672	0.05	34.1
23/4/87	0.173	0.884	0.005	26.6
21/8/87	0.133	0.885	0.005	34.6
21/11/87	0.200	0.956	0.0007	23.0
5/1/88	0.184	0.961	0.002	25.0
28/2/88	0.211	0.979	0.0002	21.8
7/5/88	0.112	0.88	0.006	41.1
8/5/88	0.054	0.881	0.006	85.2
2/7/88	0.134	0.936	0.002	34.3
5/1/89	0.216	0.899	0.004	21.3
6/1/89	0.120	0.957	0.0007	38.3
<b>AVERAGE</b>	<b>0.153</b>	<b>(<math>\pm</math> 0.014)</b>		<b>34.4</b>

A complicating factor not accounted for at Bicheno was an effect produced under conditions of 1.5+ m swell. Close to the bottom, swell action was very evident in the ebbing of the water across the reef face and it

raised sediment in a cloud of murky water 2+ m above the substrate. This would have cut the amount of light available to the bottom on some occasions and may not have been accounted for by the attenuation readings.

### Radiation

To estimate the amount of radiation available to the plants at the two different sites, Total Global Radiation figures as measured at Hobart Airport were utilized. Both sites are less than 1° latitude distant from Hobart (Bicheno north, George III Reef, south) so differences are expected to be small. The following formula was used to calculate incident radiation for a specified depth:

$$E = I_m \cdot C \cdot L \cdot e^{-kd} \text{ (Weinberg 1976)}$$

where  $I_m$  = total daily radiant energy at the water surface for the month  $m$ ,  $C$  = the correction factor to convert total surface radiant energy values (300-3000 nm) to values corresponding to underwater spectral distribution,  $L$  = conversion constant to allow for apparent albedo i.e. the amount of energy lost by reflectance from the surface and  $k$  is the mean attenuation coefficient for the period of the study at the two different sites. Results are presented in Figure 2.14.

### Wave Action/Water Motion

Swell and sea states are depicted in Figure 2.15 for both sites. These are the synopsis of more than 1200 recordings/year made at each of the lighthouses. Average sea state for Bruny Is is 3.13 ( $\pm 0.05$ ) m, while average swell is 2.70 ( $\pm 0.05$ ) m. The adjusted value for George III Reef being 1.54 ( $\pm 0.03$ ) m. Average sea state for Eddystone is 2.82 ( $\pm 0.05$ ) m and swell, 1.57 ( $\pm 0.05$ ) m. Adjusted swell states at George III Reef appeared to be a good approximation of that experienced in the field. The average swells

experienced at George III Reef and at Bicheno would thus appear to be very similar.

Figure 2.16 a indicates the distribution of swell sizes between the two sites. At George III Reef, there is an even distribution, with a consistent swell size of 2-3 m. At Bicheno however, there are peaks at 1-2 m, 3-5 m and 6+ m. This demonstrates that while averages indicate similar swell sizes at the two sites, the actual swells experienced may be very different in effect. The size distribution indicates inconsistent swells and of a more destructive nature on the east coast at Bicheno compared to George III Reef.

A further complicating factor is that of local topography at each site. Bicheno had an even gradient facing into the swell, whereas the George III Reef site was at 90° - 180° to the prevailing swells (backside of the Reef) and within a complex-reef system, this may have altered local conditions further. Figure 2.16 b shows swell direction for George III Reef.

Currents of up to 2 knots (estimated, equal to top speed of swimming with flippers) were often experienced over the top of George III Reef, travelling either south-north or north-south depending on prevailing winds or tides. Rarely was there not some form of water motion at George III Reef evident from the well mixed state of the waters demonstrated by the results of nutrient analyses.

At Bicheno, particularly in late summer after a prolonged period of low swells and sea-state, water movement was experienced as being negligible, this resulted in some stratification near the site, noted on 28 Feb 1988 as a noticeable thermocline in approximately 13-15 m of water. This is believed not be of regular occurrence however but should be considered if further studies of this nature are to be done in this area.

## Tides

Tidal range at both sites from MLWS to MHWS is less than 1.5 m. However, meteorological conditions can cause this range to increase.

## DISCUSSION

### Macroalgal Communities

The dominant understory species associated with *Macrocystis* at both the sites are very different. At George III Reef, the dominant species is *Plocamium dilatatum*, a foliose red 20-30 cm in height. *Ecklonia radiata* plants, while present, are relatively few. At Bicheno, the predominant plant species in shallower waters (4-12 m deep) on flat surfaces is a species of *Halopteris*, a hardy small brown alga. This may be a reflection of its ability to withstand scour and burial from the mobile sand on the reef. *Phyllospora comosa* is plentiful on top of raised surfaces and boulders. In deeper waters, *Ecklonia* becomes the dominant plant. *Plocamium dilatatum* although present is rare.

On other Tasmanian coastlines, species likely to be commonly associated with *Macrocystis* are *Lessonia corrugata*, *Cystophora* spp., *Sargassum* spp. and *Xiphophora gladiata* of the brown algae, *Sonderopelta coriacea*, *Rhodymenia australis*, *Callophyllis* sp. and *Phacelocarpus* sp. of the red algae and *Caulerpa* spp. and *Codium* spp. of the green algae.

Of the *Macrocystis pyrifera* forests investigated world-wide, similarities in the patterns of stratification have been noted (Barrales and Lobban 1975). They consist principally of four layers

1. the upper *Macrocystis* canopy, usually in 3-20 m of water followed by
2. an upper-middle layer of (0.5)1-2(15) m in height consisting of long stiped brown kelps of either the Laminariales or Fucales,

3. a lower-middle layer with algae 5-40 centimetres in height, consisting of principally red algae with occasional browns and greens.

4. The lowest layer consisting of turf forming species and encrusting corallines.

In Tasmania, the species making up these layers can vary greatly from place to place depending largely on the depth, exposure, substrate type and slope and density of the *Macrocystis* forest (personal observation). This agrees with findings elsewhere. Devinny and Kirkwood (1974) found eleven algae unique to wave exposed beds, and thirteen unique to sheltered beds in the vicinity of Monterey Peninsula in California. They could find no species that were associated only with *Macrocystis* canopies. Rather, the sub-canopy flora was more a reflection of the change between floras on the shallow and deeper sides of the forest. The presence or absence of *Macrocystis* however has been found to affect the species compliment of the smaller algae in southern south America (Santelices and Ojeda 1984a).

*Macrocystis* canopies are also often transient and their presence or absence can affect not only associated species types but also quantities in their understory. North (1971) found an approximately seven-fold decrease in understory algal biomass under a thick canopy compared with a site just outside of it and Santelices and Ojeda (1984a) noted an increase in biomass of understorey species when the canopy was removed in South America. Floras associated with *Macrocystis* however share similar environmental tolerances and on this basis a comparison can be made of the floras associated with *Macrocystis* forests, world-wide.

#### Comparison with *Macrocystis* forests elsewhere

Table 2.3 (pp. 71 & 72) contains details concerning the upper and lower understory layers of *Macrocystis pyrifera* forests in North and South

America, New Zealand and Tasmania. The table concerns principally longer-lived common macroalgal species at the different localities in or under the *Macrocystis*, not including the smaller turf algae, ephemerals, encrusting or epiphytic algae (many of which are incidentally, cosmopolitan).

Conspicuous species that are common to all *Macrocystis* communities belong to the genera *Codium*, *Corallina*, *Desmarestia*, *Dictyota*, *Callophyllis*, *Plocamium* and *Rhodymenia*. These are likely to be species that disperse readily most likely through attachment to boats, ships or even floating *Macrocystis* plants (Edgar 1987).

The upper-understory species of the northern hemisphere *Macrocystis* forests are noted for their high species diversity (Dayton 1985). They consist of many members of the Laminariales. Of these the Lessoniaceae are believed to have originated in the northern hemisphere, with *Macrocystis* and *Lessonia* migrating across the equator possibly during the last ice age. The Caulerpales in contrast, are well represented in the southern hemisphere and Southern Australia is viewed as their geographical origin (Calvert *et al.* 1976).

The decreased species diversity of the South American flora with respect to the north American flora has been noted by Dayton (1985), Barrales and Lobban (1975) and Santelices and Ojeda (1984a). Dayton (1985) has attributed this to the relatively recent invasion of species to this shoreline. It is believed Pleistocene ice sheets in periods of much lower sea levels scoured the coastal areas of southern South America leaving it relatively barren. Existing communities are thus composed of species that have invaded during the last 20 thousand years of the Holocene. This is consistent with the observation that those algal species present, are good dispersers (esp. *Durvillaea antarctica* and *Macrocystis pyrifera*). The New Zealand and Australian floras have many similarities to each other which is

not surprising considering their proximity. They also are rich in comparison to the South American flora. Womersley (1981) has regarded the southern Australian coastline as having one of the richest cold temperate floras in the world, on a par with the Japanese region and Pacific North America. This, in contrast to the situation in South America, can be attributed to the relative geological stability of the coastline over a long period of time (probably 20-30 million years, Knox 1978).

Generally, species similarities between the widely separated forests can be attributed to species that readily disperse, either by fragments of drifting reproductive material or by rafting on holdfasts, logs or other materials. Differences are attributable to the geological stability of the coastlines and barriers arising from oceanic circulation patterns.

#### Light energy

Macroalgae growing at different depths in the sea require different quantities of PAR (Lüning 1981). Intertidal species require  $400-600 \mu\text{mol m}^{-2}\text{s}^{-1}$  (full sun is approximately  $2000 \mu\text{mol m}^{-2}\text{s}^{-1}$ ), upper- and mid-sublittoral species saturate with  $150-250 \mu\text{mol m}^{-2}\text{s}^{-1}$ , and deep-sublittoral species require less than  $100 \mu\text{mol m}^{-2}\text{s}^{-1}$ . The distribution of species at the two different sites of this study accords well with these findings in relation to the estimated light fields. Greater light radiation is likely to be available at Bicheno than at George III reef at similar depths.

#### Wave action, water motion

Overall, it would appear that while intrinsically the sites seemed similar in terms of exposure to wave action, there were certain differences in the pattern that might have large effects on the communities present. At George III Reef the swells appear to have been fairly consistent and the site was not directly exposed to incoming swells. The swells at Bicheno however

were variable and the site is subject to intermittent large swells with a potentially destructive effect on the biotic communities. This effect would have been exacerbated by the aspect of the site. This for example, may explain the patchy nature of the distribution of the algae at Bicheno in comparison to George III Reef.

Also the presence of sand on the reef at Bicheno which, in combination with the flat reef and the swells, has a scouring action on the rock surface. This may contribute to the effect of concentrating the majority of the algal biomass, particularly the *Phyllospora comosa* on raised rocky surfaces. The algae in the depressions and gullies were restricted. This effect appeared to decrease with depth.

#### Nutrient Regimes

Of the three nutrients measured, nitrate would appear to be the most limiting as it periodically approaches zero. This is most evident in the CSIRO results for the shallower water (10 m depth) at both Maria Is. and Storm Bay. Due to the intermittent sampling regime at Bicheno and George III Reef it is difficult to confirm a similar scenario to Maria Is. and Storm Bay respectively however the high correlation of temperature and salinities would appear to confirm similar water masses and consequently similar nutrient regimes. These findings are in agreement with those of Rochford (1975 a) for the south and east coasts of Tasmania.

Some indication of the mechanism for nutrient enrichment of coastal waters may be obtained from combined Meteorological and CSIRO results. Swell and sea state figures show maximum values over the winter period which agrees with higher nutrient concentrations derived as a result of greater mixing of surface with deeper waters. A significant correlation is obtained ( $r=0.39$ ,  $p<0.05$ ) for the difference between the temperature at 10m and at 50 m depth in Storm Bay and the average swell size as recorded at



Bruny Island Lighthouse. Rochford (1984) demonstrated a similar relationship for the waters off Maria Island where a mean temperature difference of zero degrees between waters at 0m and 50m during winter corresponded to higher nitrate levels with a mean value of  $2\mu\text{M}$   $[\text{NO}_3]$  and a 1.5 degree temperature difference in summer corresponded to low nitrate levels.

Temperature demonstrates a negative relationship with nitrates at 10 and 20 m depth for the Storm Bay data ( $r = 0.671$  and  $0.595$  respectively,  $p = .0001$ , Figs 2.18 a and b) with almost no recorded nitrate levels for waters over  $14.5^\circ\text{C}$  at 10 m depth. The limited data from Maria Island is not sufficient for correlation but the graphs in Figures 2.18 c and d appear to support a similar relationship here as well.

In 1985 & 1986, the higher nutrient period extended later into the year for George III Reef and Storm Bay. This agrees well with an increased incidence of south-easterly swells for these years (Fig. 2.16 b). This compares with Harris *et al.* (1991) who demonstrated a strong correlation between the annual total of zonal westerly winds and the timing and duration of the spring bloom in Tasmanian coastal waters at Maria Island.

Harris *et al.* (1991) have interpreted the patterns of temperature, salinity and nutrients measured at the Storm Bay site as being largely wind driven. The cooler winters and summer of 1986-87 were marked by higher than normal wind speeds. These turnover water from lower in the water column and maintain cooler temperatures and higher nutrient levels. The warmer summers and winter 1988-89 were distinguished by a reduction in the wind stress. The usual depth of mixing is  $\sim 300\text{m}$  (Harris *et al.* 1987a, b) whereas measurements of the offshore mixed layer depth in the warm winter of 1988 indicated a mixed layer of only 75-100m. Nitrate and phosphate levels in the winter of 1988 were half those of the previous year.

Very low phosphate concentrations in March in 1985 and 1988 coincide with the incursion of the subtropical waters of the EAC at Storm Bay.

Despite some anticipated differences between the east and south coasts in terms of nutrient concentrations, averaged nitrate concentrations for the water column for the period 1985-6 for Storm Bay and Maria Island demonstrate little difference between the two areas (see Fig. 2.17). This may be expected to hold true generally, for while Bicheno is under the influence of warmer subtropical currents, it is also closer to the continental shelf and deeper water. As a result it is more likely to benefit from nutrient laden incursions brought up from deeper waters as a result of mixing. George III Reef and Storm Bay are in semi-enclosed embayments and would not benefit from mixing as readily. Results of nutrient analysis off Maria Island are not available for 1987-88 from CSIRO, making a more comprehensive comparison of the southeast and south coasts difficult for the period we are interested. Monitoring at George III Reef and Bicheno in 1988, shows the effect of the EAC, and a warm winter at both sites also indicating little difference in water masses between the sites on the east and south coasts during the period of this study.

#### Oceanic Circulation around the East and South Coasts of Tasmania.

The Maria Is monitoring station has been run since 1946 by CSIRO. This, in conjunction with the Storm Bay monitoring station, data from local oceanographic cruises, monitoring stations in Bass Strait and the mainland and now information from satellite images has enabled a reasonably comprehensive picture to be constructed of oceanographic patterns on the east and south-eastern coasts of Tasmania.

Coastal waters of eastern and south-eastern Tasmania have proven to be a complex mixture of subantarctic and subtropical water masses, with the subtropical convergence being the boundary between these water masses.

The convergence, as measured in the surface currents, runs east from the from east coast of Tasmania towards New Zealand.

Wyrski (1960) showed that the flow of currents around Tasmania is a balance of the flow from the south west, driven by the West Wind Drift in the Southern Ocean, and the flow of the East Australian Coast (EAC) Current from the north-east. Differences between summer and winter can be attributed to the more northerly position of the high-pressure areas in the winter allowing westerly winds to sweep across the Great Australian Bight, driving subantarctic waters and thus the subtropical convergence up the east coast. How far this convergence extends northwards in the winter and southwards in the summer varies from year to year depending on pressure differences between the equatorial and temperate regions. Waters of subtropical and subantarctic origin can be recognized by distinctive temperature-salinity signatures although in the vicinity of the convergence, warming of the subantarctic waters and cooling of the subtropical waters often makes interpretation difficult (see table 2.4 ).

**Table 2.4.** Temperature - Salinity characteristics of the main water masses found off the east coast of Tasmania (from Rochford 1975 b).

	Temperature (°C)		Salinity (‰)	
	Winter	Summer	Winter	Summer
EAC	16	24	35.3	35.6
Central Tasman	17	22	35.8	36.0
Subantarctic	11	13	34.5	35.1

Both nutrients and the productivity of these waters have been shown to be closely related to the hydrological oceanography; the northern subtropical waters are not only warmer and more saline but low in nutrients, biomass and productivity, whereas the subantarctic waters are comparatively less saline, cooler, richer in nutrients and more productive.

For the forty years CSIRO have been monitoring the waters off Maria Island maximum annual temperatures have increased steadily to be 1°C higher on average (Harris *et al.* 1988). Incursions of the EAC have concurrently been extending further south. In early 1988, the EAC affected waters well south of Tasmania. This is reflected in the high temperatures and salinities and low nutrients recorded at both Bicheno and George III Reef (see Figs 2.9 and 2.10) for that period.

Pre-mid 1970's, El Niño Southern Oscillation (ENSO) events were evident in Tasmania as a latitudinal 3° northward shift of the subtropical convergence evidenced by warmer winter minimum and cooler summer maximum. Since 1975 however this association has broken down. It is believed the Maria Island Station may be becoming less sensitive to the ENSO stimulus as a result of the increased influence of water of a northerly origin (Harris *et al.* 1987). These long term changes are likely to affect the macroalgal flora in terms of productivity and species compliment. Tasmania has a few macroalgal species endemic to the state, mostly recognized as sub-antarctic e.g. *Codium dimorphum*, *Lessonia corrugata* and *Macrocystis pyrifera* (endemic relative to the Australian mainland). If the waters are to warm around the state, then the continued existence of some of these species may be threatened in Tasmanian waters.

## SUMMARY

Differences between George III Reef and Bicheno:

Bicheno has warmer more saline waters.

Nitrogen is most likely to be limiting to plant growth at both sites but any differences in the availability of this nutrient at the two sites were not detectable in this study.

Analysis of sea state demonstrates that while average swell sizes are similar between the Bicheno and George III sites, the Bicheno site is open to more variable swells and of a potentially destructive nature exacerbated by the aspect of the site and its relatively steep shores facing into the prevailing swell direction.

The presence of sand on the reef means that plants at Bicheno are potentially subject to scour. This effect may have been enhanced in early 1988 by the disappearance of the *Macrocystis* forest that can ameliorate the effects of water motion resulting from swell action.

The disappearance of the *Macrocystis* canopy late in 1987 at George III Reef is likely to have increased the amount of light available to understory plants by 25%.

Measurement of light attenuation indicates clearer waters at Bicheno by as much as 50% for most of the year.

There is on average more daylight per day at Bicheno.

Monitoring of sea-water in early January 1987 revealed the influence of the East Australian Current at all sites and differences between the sites in terms of the prevailing nutrient regime over the study period were small.

Longer term (40+ years) monitoring shows an increase in water temperatures on Tasmania's east coast coincident with an increasing incidence of the East Australian Current. This may have long term affects on community composition.

**Table 2.1** Correlation between physical parameters of temperature, salinity and nutrient concentrations measured at George III Reef and the same measured at 10, 20, 30 and 40 m depth in Storm Bay for the period 1985-1988. N = 27, 23, 20, 23 respectively for temperature, salinity, nitrate and phosphate.

	GEORGE T	TEMP10M	TEMP20M	TEMP30M	TEMP40M
GEORGE T	1				
TEMP10M	.923	1			
TEMP20M	.926	.978	1		
TEMP30M	.874	.936	.946	1	
TEMP40M	.891	.947	.954	.992	1

	GEORGE S	SAL-10M	SAL-20M	SAL-30M	SAL-40M
GEORGE S	1				
SAL-10M	.694	1			
SAL-20M	.84	.597	1		
SAL-30M	.826	.588	.879	1	
SAL-40M	.797	.642	.813	.951	1

	GEORGE-N	NIT-10M	NIT-20M	NIT-30M	NIT-40M
GEORGE-N	1				
NIT-10M	.512	1			
NIT-20M	.552	.835	1		
NIT-30M	.523	.534	.828	1	
NIT-40M	.401	.345	.656	.939	1

	GEORGE P	P04-10M	P04-20M	P04-30M	P04-40M
GEORGE P	1				
P04-10M	.426	1			
P04-20M	.491	.288	1		
P04-30M	.374	.215	.872	1	
P04-40M	.448	.195	.648	.866	1

Table 2.3 Upper and lower understory species of *Macrocystis pyrifera* forests for a number of studies conducted world-wide.

	TASMANIA	NEW ZEALAND	NEW ZEALAND	ARGENTINA
	Sanderson 1990	Stewart Is Adams 1974	Kaikoura Coast South & Adams 1976	Barrales & Lobban 1975
<u>HIGH UNDERSTORY</u>				
DURVILLAEALES	<i>Durvillaea</i> sp.	<i>Durvillaea</i> sp.	<i>Durvillaea</i> sp.	<i>Durvillaea</i> sp.
FUCALES	<i>Cystophora</i> spp. <i>Phyllospora comosa</i>	<i>Carpophyllum flexuosum</i> <i>Cystophora</i> spp <i>Landsburgia quercifolia</i> <i>Marginariella</i> spp. <i>Sargassum</i> spp.	<i>Carpophyllum</i> <i>maschalocarpum</i> <i>Landsburgia quercifolia</i> <i>Sargassum</i> spp.	
LAMINARIALES	<i>Ecklonia radiata</i> <i>Lessonia corrugata</i>	<i>Ecklonia radiata</i> <i>Lessonia variegata</i>	<i>Ecklonia radiata</i>	<i>Lessonia</i> spp.
<u>LOW UNDERSTORY</u>				
CHLOROPHYTA	<i>Caulerpa flexilis</i> <i>Sporochnus comosus</i> <i>Cystophora</i> spp. <i>Xiphophora gladiata</i>	<i>Caulerpa brownii</i> <i>Dictyota</i> sp. <i>Halopteris funicularis</i>	<i>Caulerpa brownii</i> <i>Glossophora kunthii</i>	<i>Codium vermilara</i> <i>Dictyota</i> sp. <i>Zonaria</i> spp.
PHAEOPHYTA	<i>Callophyllis</i> spp. <i>Carpopeltis phyllophora</i> <i>Crassilingua marginifera</i> <i>Mastophora canaliculata</i> <i>Sonderopelta</i> sp. <i>Phacelocarpus</i> sp. <i>Plocamium angustum</i> <i>Plocamium dilatatum</i> <i>Plocamium mertensii</i> <i>Ptilonia australasica</i> <i>Rhodymenia australis</i> <i>Thamnoclonium dichotomum</i> <i>Rhodymenia</i> spp.	<i>Ballia</i> spp. <i>Callophyllis</i> sp. <i>Corallina</i> spp. <i>Curdiea coriacea</i> <i>Delisea</i> spp. <i>Epymenia wilsonis</i> <i>Hymenena</i> spp. <i>Lenormandia chauvinii</i> <i>Myriogramme denticulata</i> <i>Plocamium</i> spp. <i>Ptilonia willana</i> <i>Rhodophyllis gunnii</i>	<i>Asparagopsis armata</i> <i>Cladymenia oblongifolia</i> <i>Craspedocarpus erosus</i> <i>Delisea</i> spp. <i>Epymenia wilsonis</i> <i>Euptilota formosissima</i> <i>Hymenena</i> spp. <i>Phycodrys quercifolia</i> <i>Plocamium</i> spp <i>Ptilonia willana</i> <i>Rhodophyllis membranacea</i> <i>Rhodymenia</i> spp.	<i>Ballia</i> sp. <i>Bossiella</i> sp. <i>Callophyllis</i> sp. <i>Ceramium</i> sp. <i>Chondria macrocarpa</i> <i>Corallina officinalis</i> L. <i>Epymenia</i> sp. <i>Gigartina</i> sp. <i>Griffithsia</i> sp. <i>Hymenena falklandica</i> <i>Lophurella</i> sp. <i>Myriogramme</i> sp.
RHODOPHYTA				

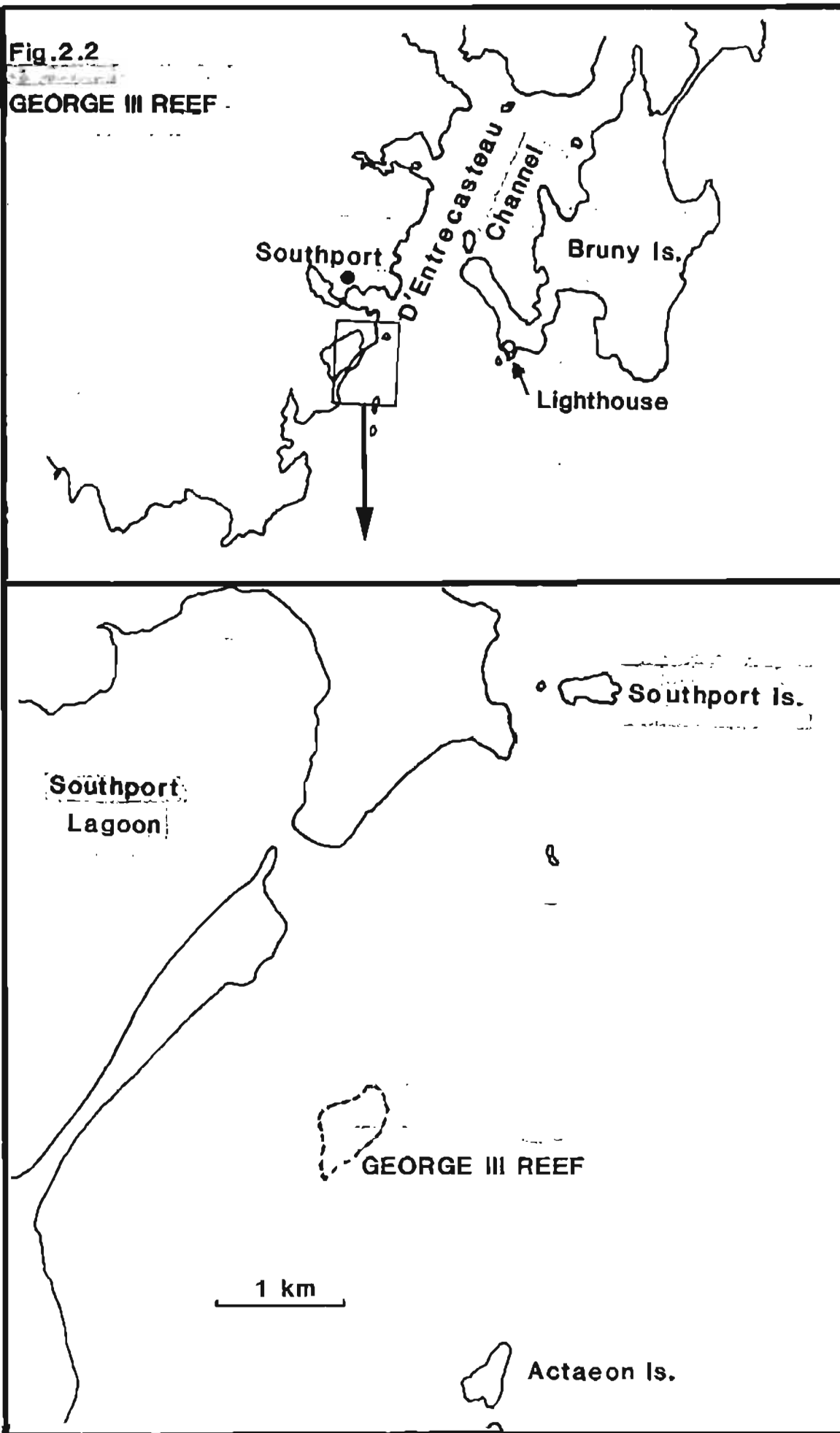
Table 2.3 cont.

	CALIFORNIA North 1971 Devinny & Kirkwood 1974 Abbott & Hollenberg 1976	CHILE Santelices & Ojeda 1984	CHILE Dayton 1985.
<u>HIGH UNDERSTORY</u>			
DURVILLAEALES		<i>Durvillaea</i> sp.	<i>Durvillaea</i> sp.
FUCALES	<i>Cystoseira osmundacea</i>	<i>Lessonia vadosa</i>	<i>Lessonia vadosa</i>
LAMINARIALES	<i>Dictyonium californicum</i>	<i>Lessonia flavicans</i>	<i>Lessonia flavicans</i>
	<i>Egregia menziesii</i>		<i>Lessonia nigrescens</i>
	<i>Eisenia arborea</i>		
	<i>Nereocystis leutkeana</i>		
	<i>Pelagophycus porra</i>		
	<i>Pterygophora californica</i>		
<u>LOW UNDERSTORY</u>			
CHLOROPHYTA	<i>Codium</i> sp.	<i>Codium</i> sp.	<i>Codium</i> sp.
PHAEOPHYTA	<i>Desmarestia</i> spp.	<i>Halopteris hordacea</i>	<i>Colpomenia</i> sp.
	<i>Dictyota flabellata</i>	<i>Zonaria</i> sp.	<i>Desmarestia</i> sp.
	<i>Pachydictyon coriaceum</i>		<i>Dictyota</i> sp.
	<i>Zonaria</i> sp.		
RHODOPHYTA	<i>Acrosorium uncinatum</i>	<i>Ballia callitrichia</i>	<i>Ballia</i> sp.
	<i>Bossiella</i> spp.	<i>Callophyllis variegata</i>	<i>Chaetangium</i> sp.
	<i>Botryoglossum farlowianum</i>	<i>Delesseria</i> sp.	<i>Dellesseriaceae</i>
	<i>Calliathron</i> spp.	<i>Epymenia falklandica</i>	<i>Gigartina</i> sp.
	<i>Callophyllis flabellulata</i>	<i>Gigartina skottsbergii</i>	<i>Griffithsia</i> sp.
	<i>Corallina</i> spp.	<i>Hymenena laciniata</i>	<i>Heterosiphonia</i> sp.
	<i>Faucheia laciniata</i>	<i>Iridaea</i> sp.	<i>Iridaea</i> sp.
	<i>Fryeella gardneri</i>	<i>Myriogramme</i> sp.	<i>Lophurella</i> sp.
	<i>Gelidium robustum</i>	<i>Phycodrys</i>	<i>Plocamium</i> sp.
	<i>Gigartina</i> spp.	<i>Plocamium secundatum</i>	<i>Polysiphonia</i> sp.
	<i>Laurencia subopposita</i>	<i>Rhodymenia</i> sp.	<i>Rhodoglossum</i> sp.
	<i>Peyssonnelia</i> spp.	<i>Spongomorpha pacifica</i>	<i>Rhodymenia</i> sp.
	<i>Plocamium cartilagineum</i>		
	<i>Rhodymenia pacifica</i>		

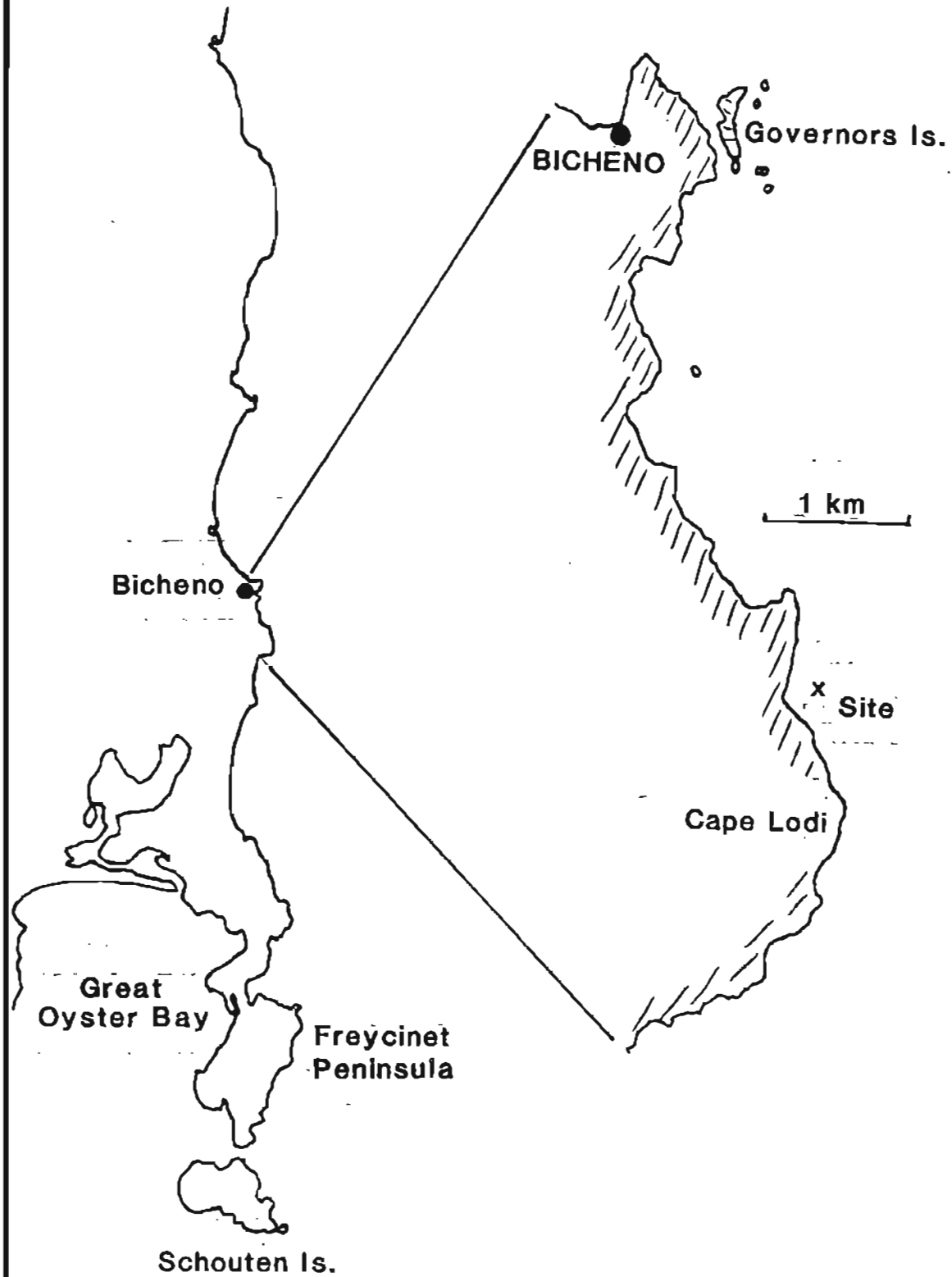


Fig.2.2

GEORGE III REEF



**Fig. 2.3 BICHENO**



**Key for Figs 2.5 and 2.7**

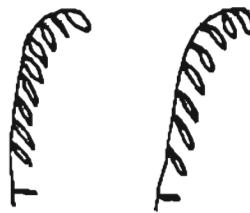
*Durovillaea potatorum*



*Phyllospora comosa*



*Macrocystis pyrifera*



*Ecklonia radiata*



Red Algae



Turf Algae



*Cystophora xiphocarpa*



*Halopteris sp.*



[illegible]

**Fig. 2.6** Percentage cover of macroalgae along transect line at George III Reef as determined, Dec. 1984 (2 cm width bar = 100 % cover, dashed lines at 5 and 10 m contours).

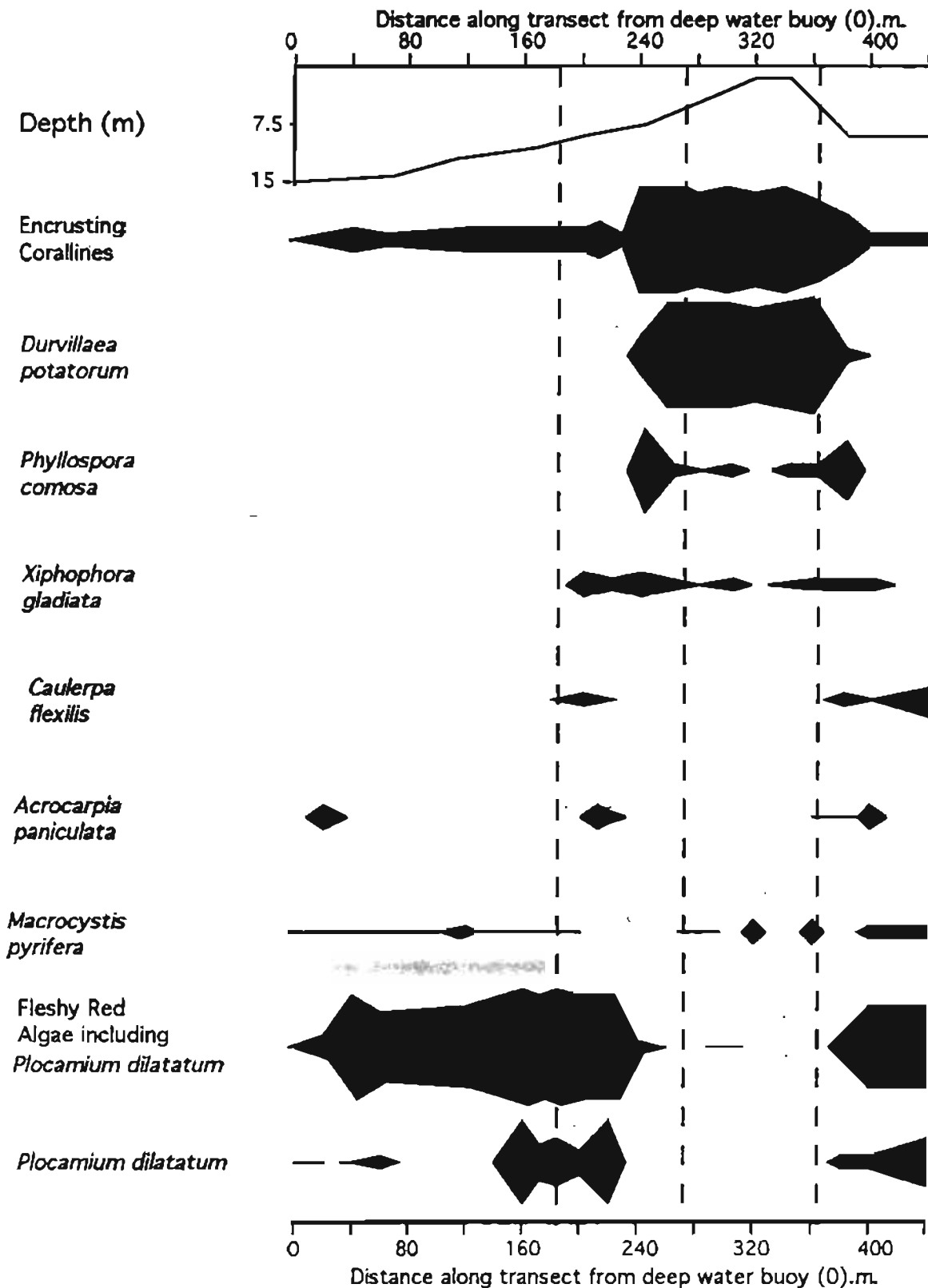
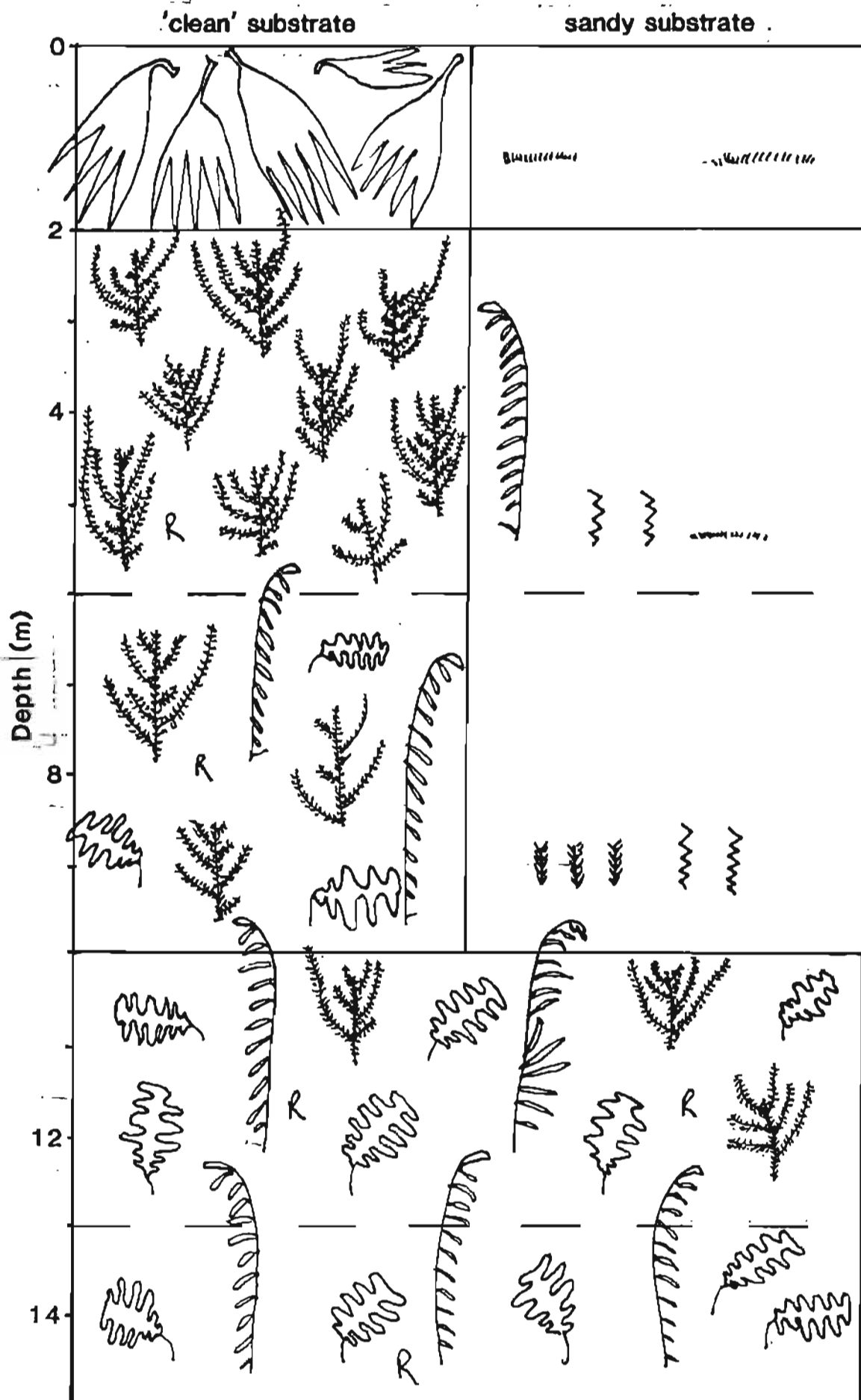


Fig. 2.7 Distribution of macroalgae at Bicheno.



**Fig. 2.8** Percentage cover of macroalgae along transect line at Bicheno as determined, Jan. 1989 (2 cm width bar = 100 % cover, dashed lines at 5 and 10 m contours).

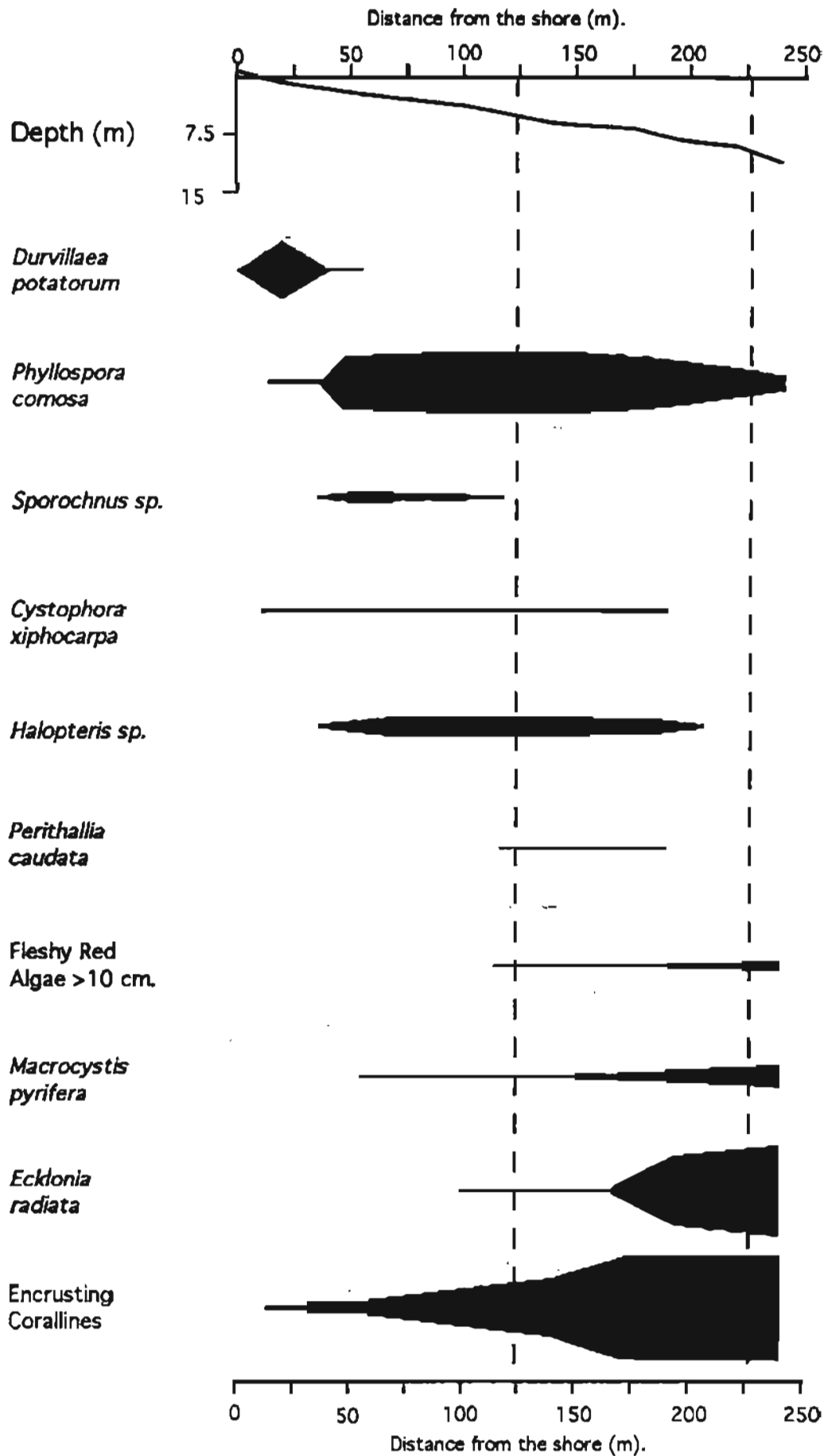
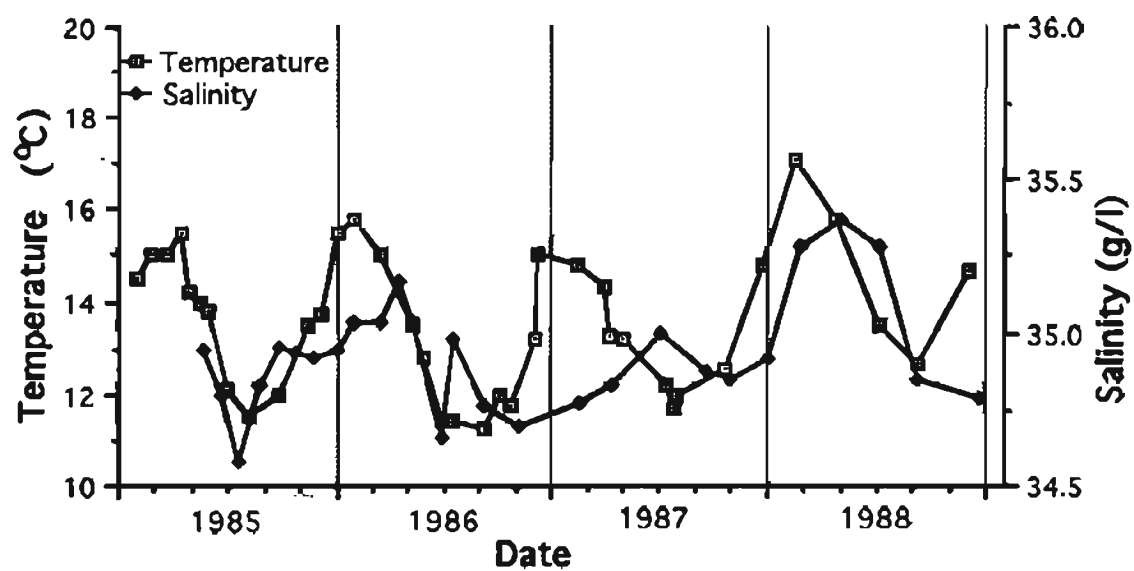
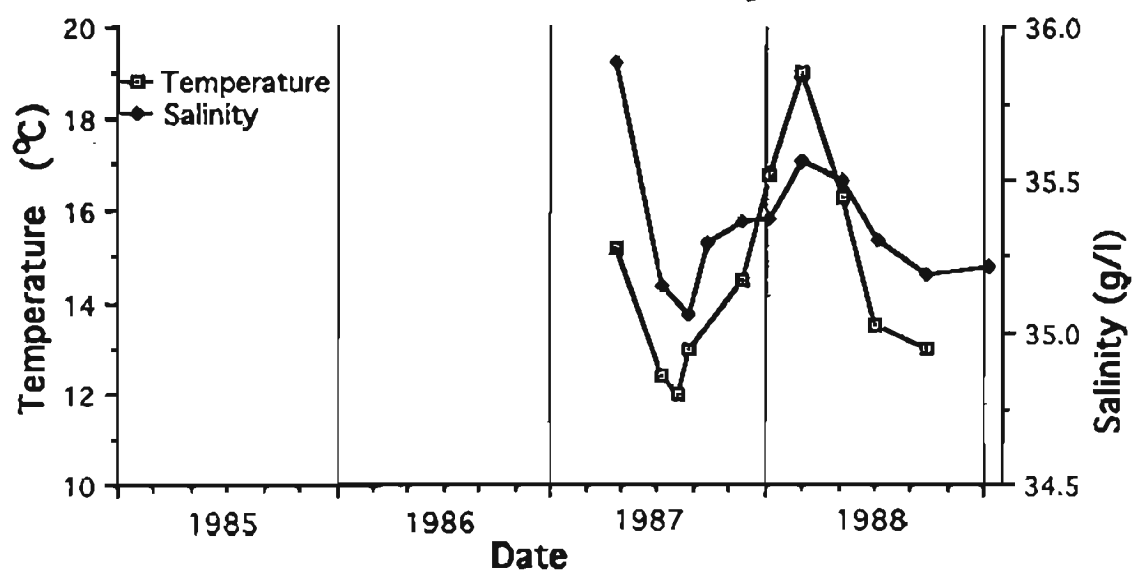


Fig. 2.9 Sea surface temperatures and salinities measured on site.

a) George III Reef.



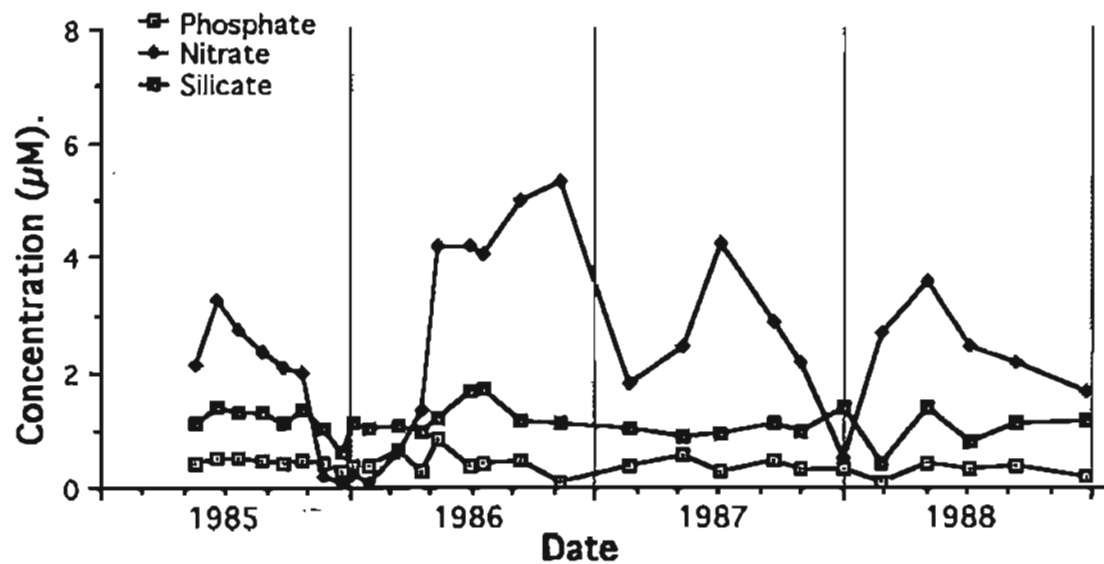
b) Bicheno



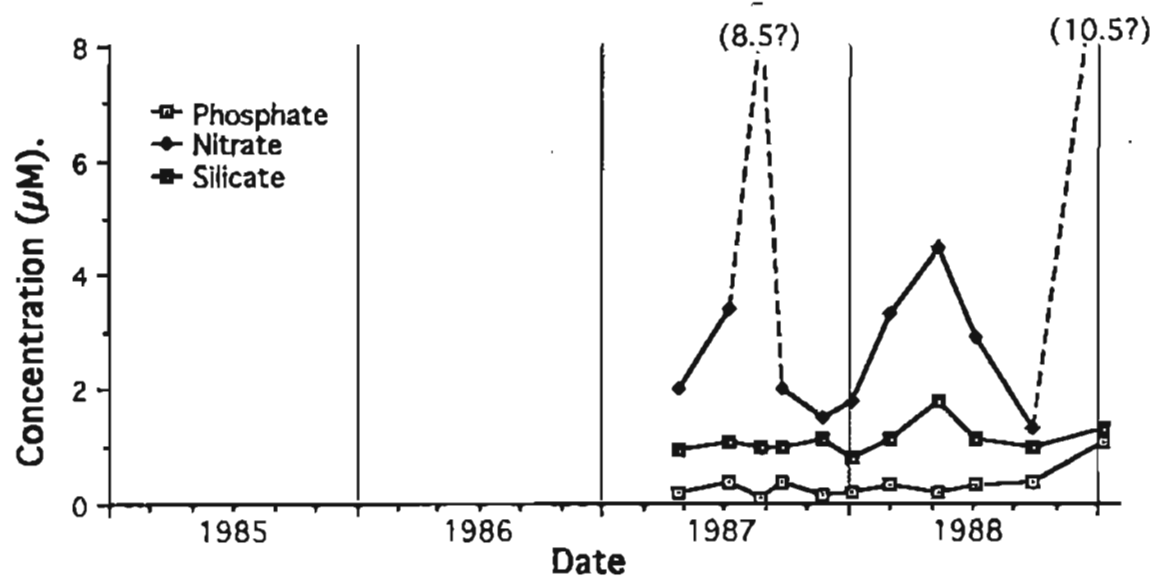


**Fig. 2.10** Sea surface phosphates, nitrates (nitrates+nitrites) and silicates as monitored on site.

**a) George III Reef**

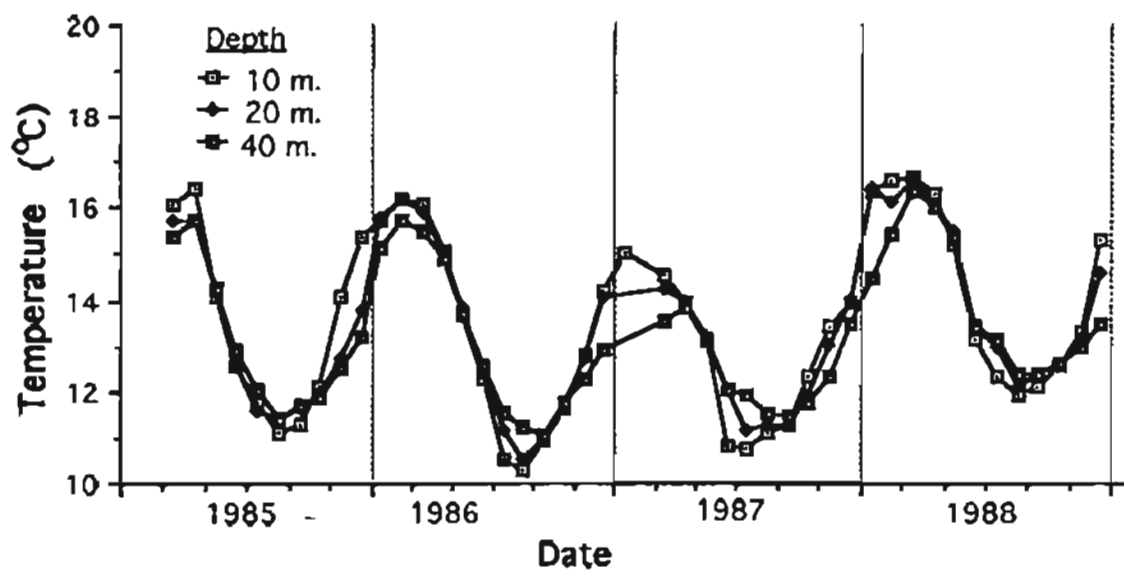


**b) Bicheno**

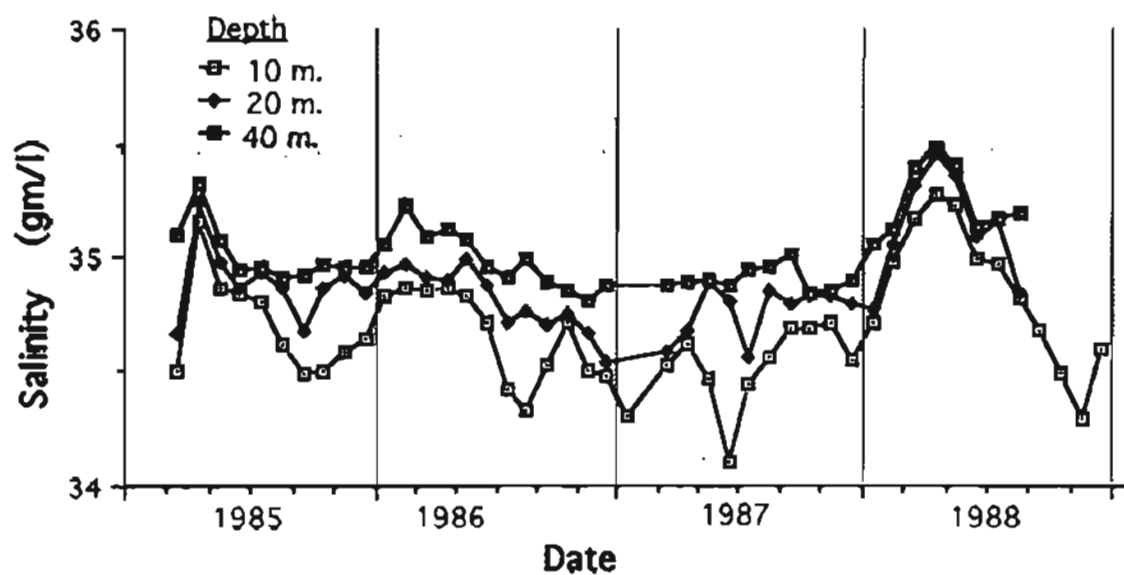


**Fig. 2.11** Variation in temperature and salinity as measured in Storm Bay at 10, 20 and 40 m depths for the period 1985-88. (Courtesy CSIRO Marine Laboratories, Hobart).

**a) Temperature**

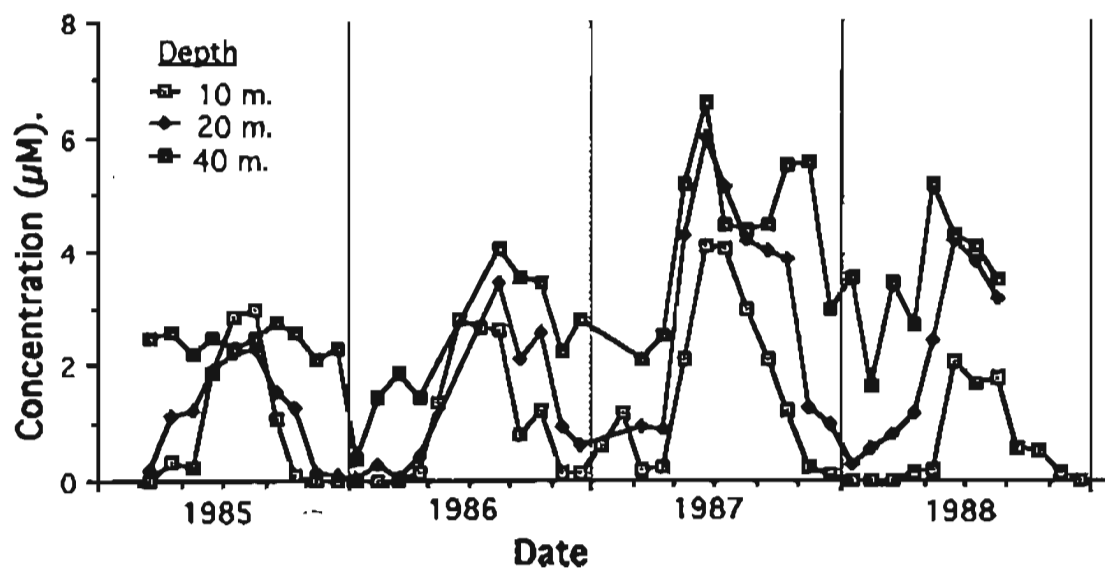


**b) Salinity**

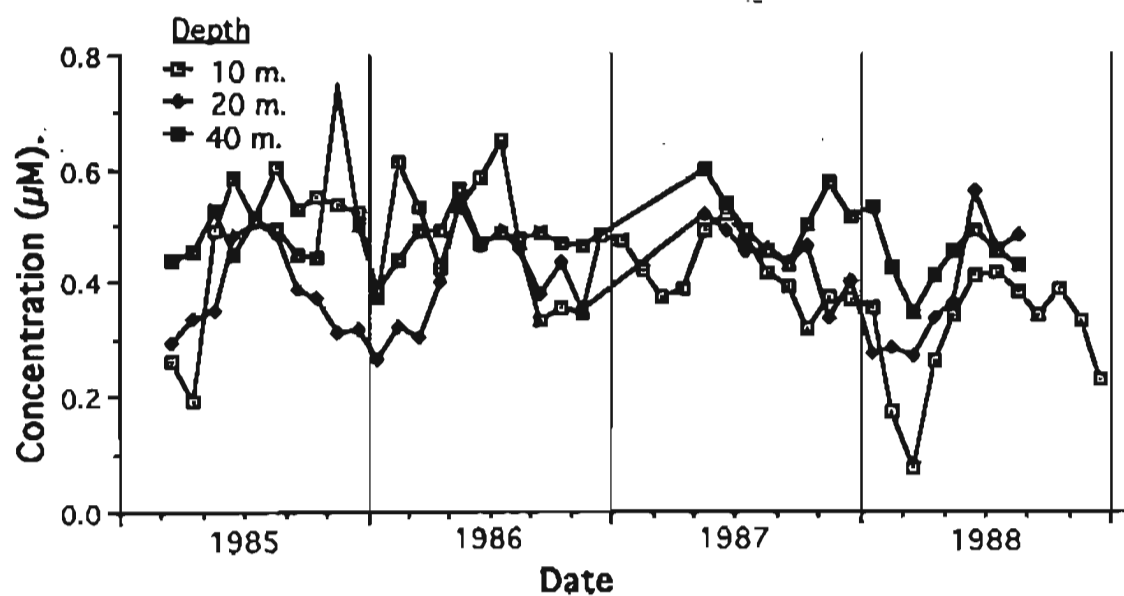


**Fig. 2.11** Variation in nitrates (nitrates + nitrites) and phosphates measured in Storm Bay at 10, 20 and 40 m depths for the period 1985-88. (Courtesy CSIRO Marine Laboratories, Hobart).

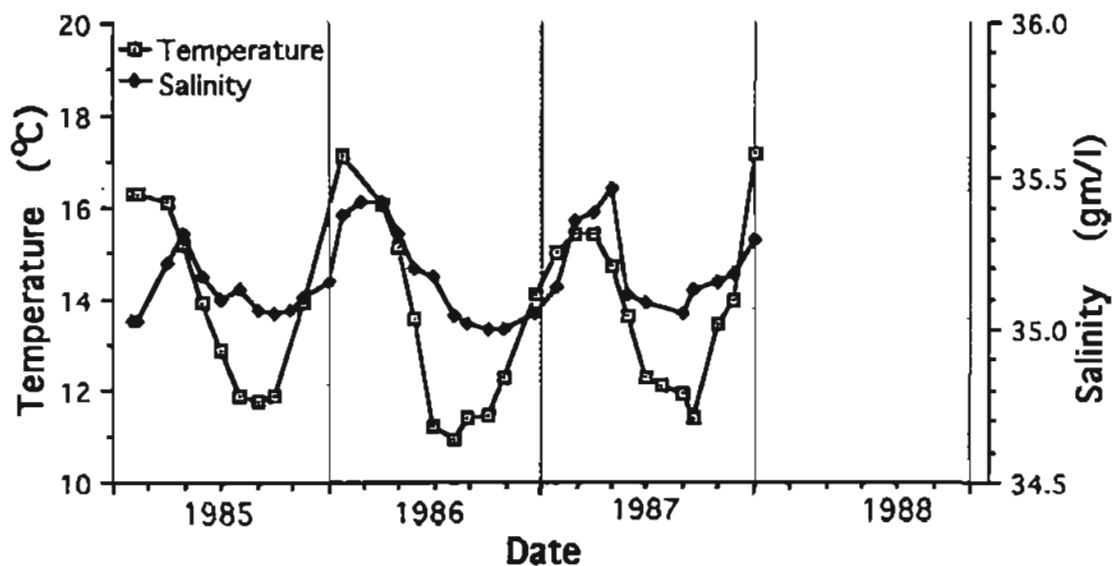
**c) Nitrates**



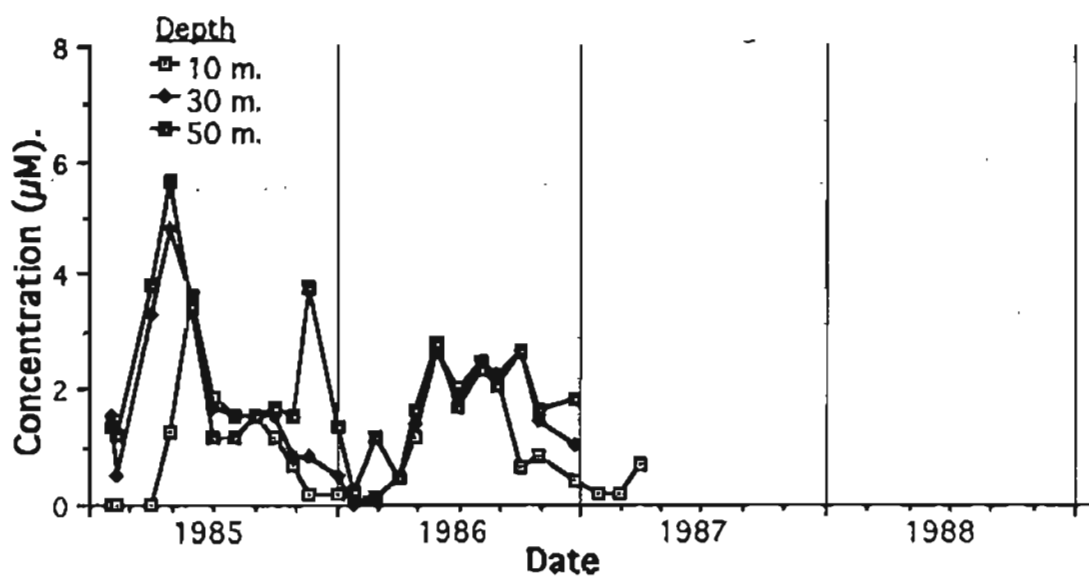
**d) Phosphates**



**Fig. 2.12 a)** Temperature and salinity variation at 10 depth off Maria Is. for the period 1985-1987 (Courtesy CSIRO Marine Laboratories, Hobart).

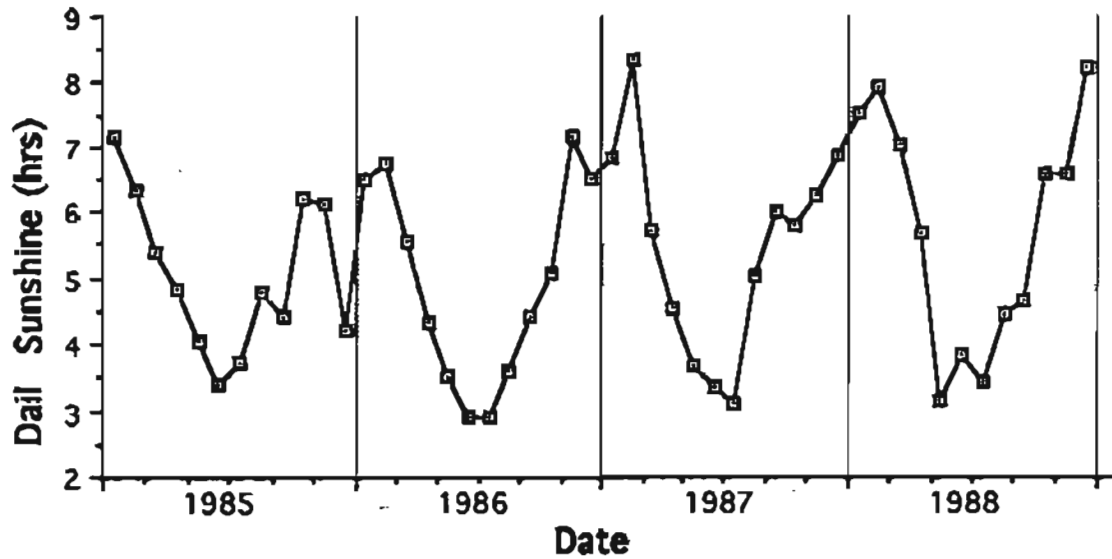


**Fig. 2.12 b)** Nitrate (nitrate + nitrite) at 10, 30 and 50 m depths off Maria Is. for the period 1985-1986 (Courtesy CSIRO Marine Laboratories, Hobart).

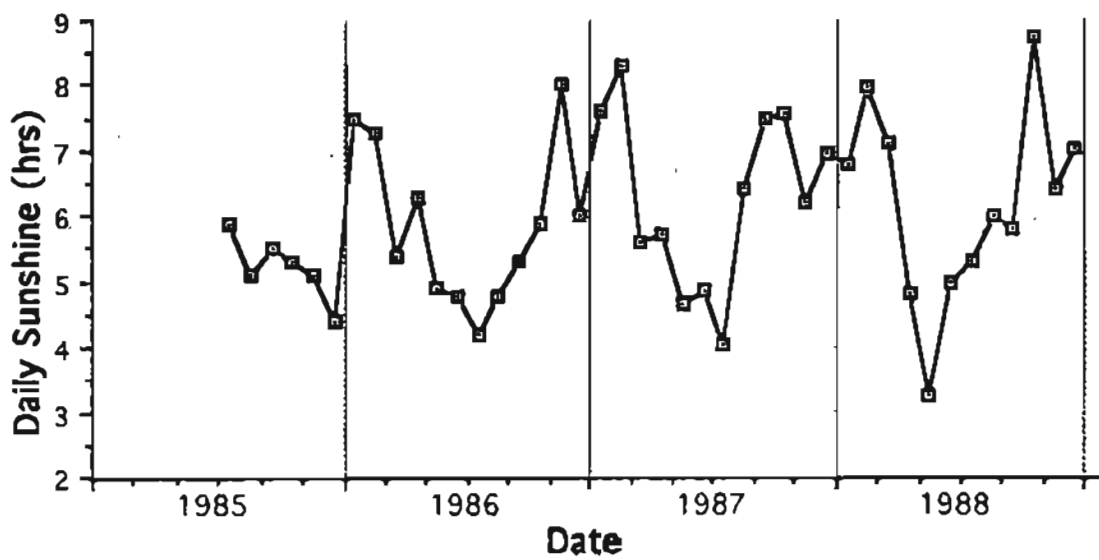


**Fig. 2.13** Mean daily sunshine as recorded at Grove weather station and Bicheno 1985-1988. (Courtesy the Bureau of Meteorology, Hobart).

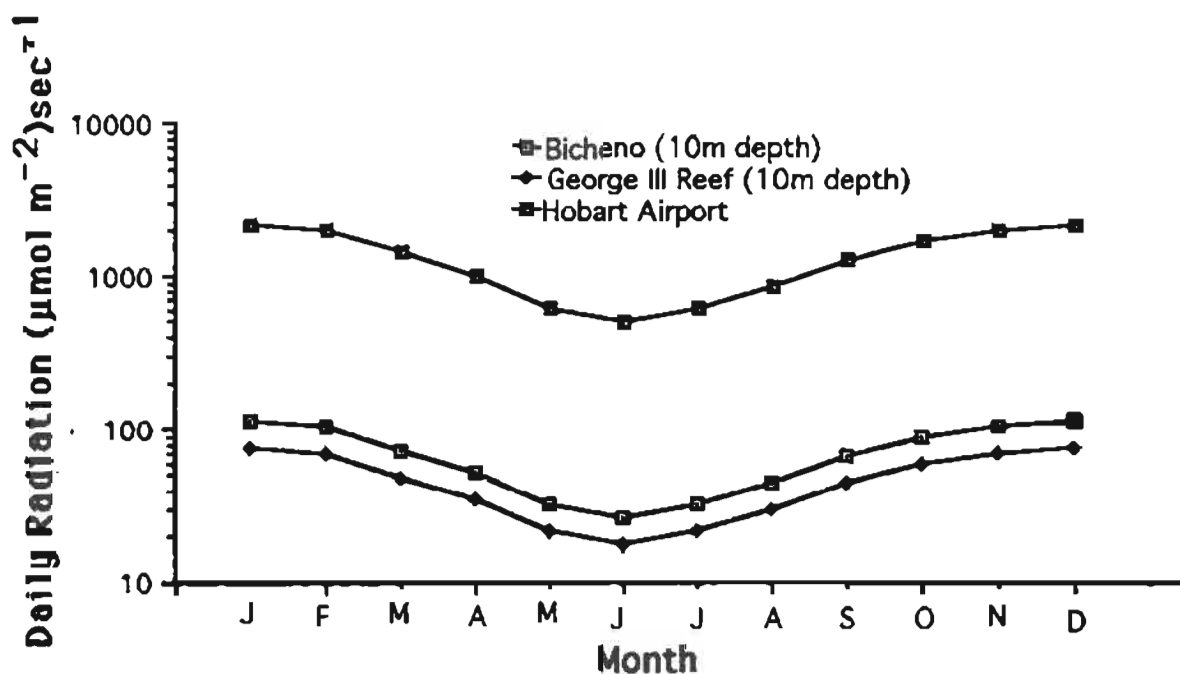
**a) Grove**



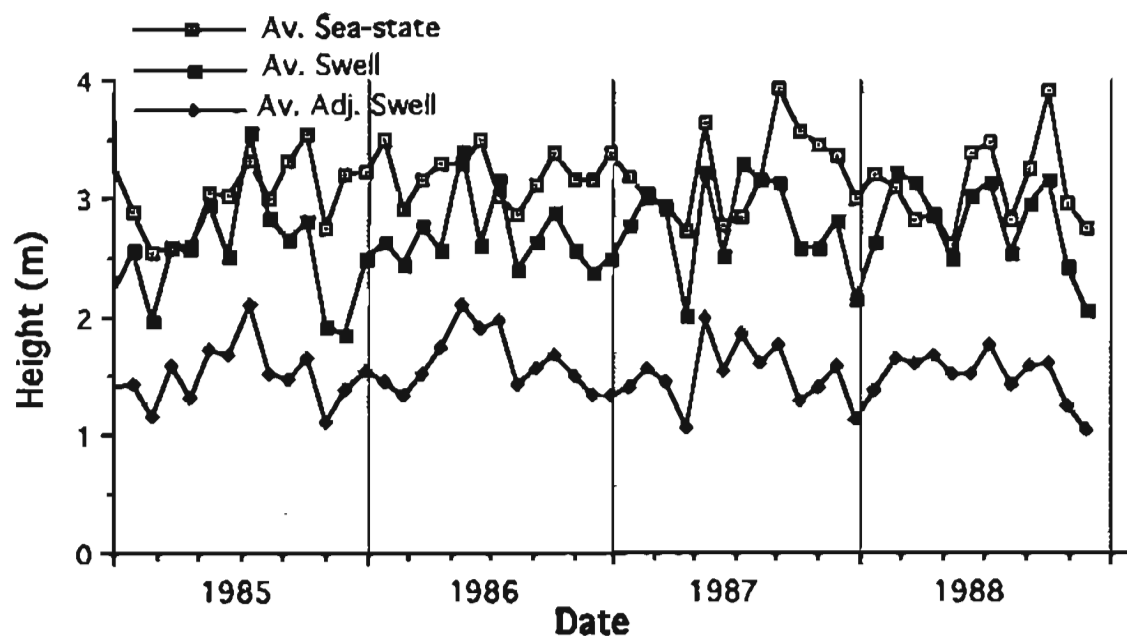
**b) Bicheno**



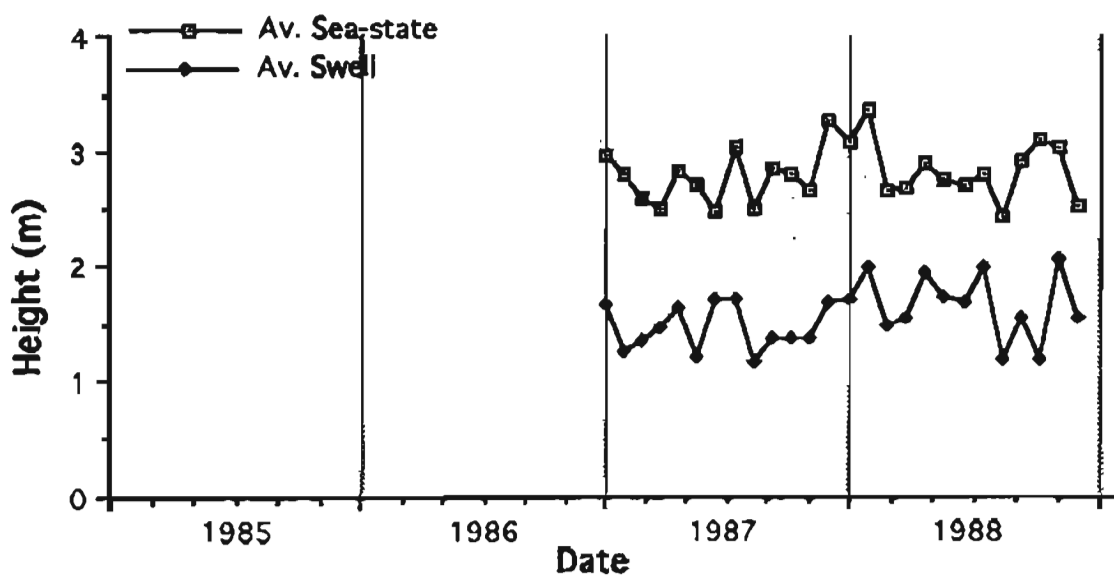
**Fig. 2.14** Monthly photosynthetic radiation levels calculated from data supplied by the Bureau of Meteorology as measured at Hobart Airport and for 10 m depth at George III Reef and Bicheno from mean extinction coefficients .



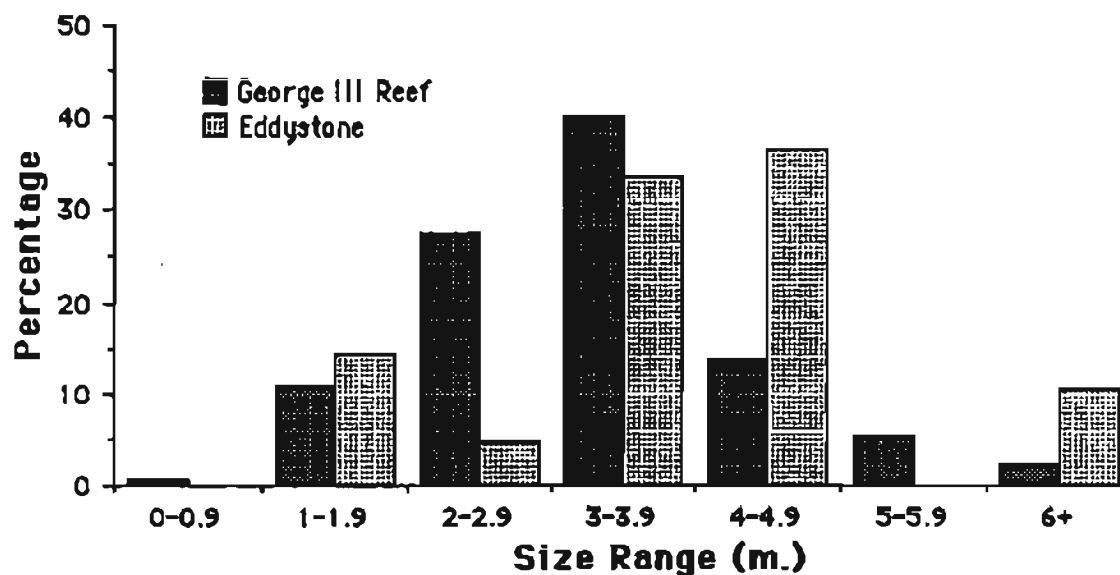
**Fig. 2.15 a)** Sea state recorded at Bruny Island Lighthouse, including swell and seastate estimates for the period 1985-1988 (Courtesy the Bureau of Meteorology, Hobart) with a calculated 'adjusted swell' for George III Reef.



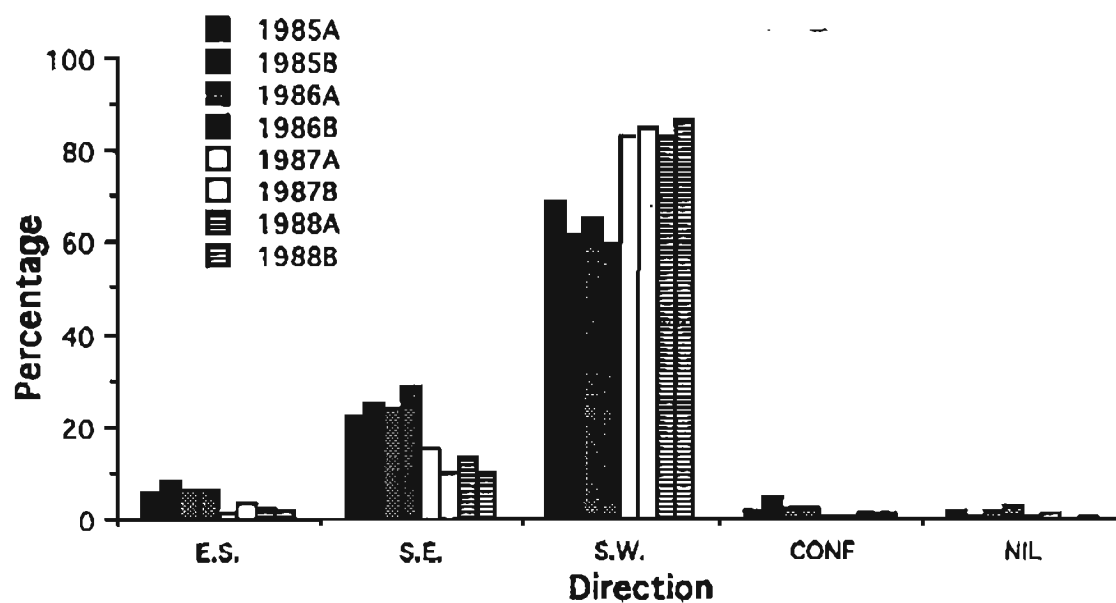
**Fig. 2.15 b)** Sea state recorded at Eddystone Lighthouse, including swell and seastate estimates for the period 1987-1988 (Courtesy the Bureau of Meteorology, Hobart).



**Fig. 2.16 a)** Breakdown of swell sizes as experienced at George III Reef and at Eddystone Lighthouse, 1985-1988, (results of 1200+ readings per year used).



**Fig. 2.16 b)** Breakdown of swell directions as recorded at Bruny Island Lighthouse for each half year period from 1985-1988.





**Fig. 2.17** Mean nitrate (nitrate+nitrite) concentrations with depth for the periods; 1985-1986 and 1985-1988 in Storm Bay and 1985-1986 for Maria Island (from CSIRO Marine Laboratory data). Vertical bars are standard error.

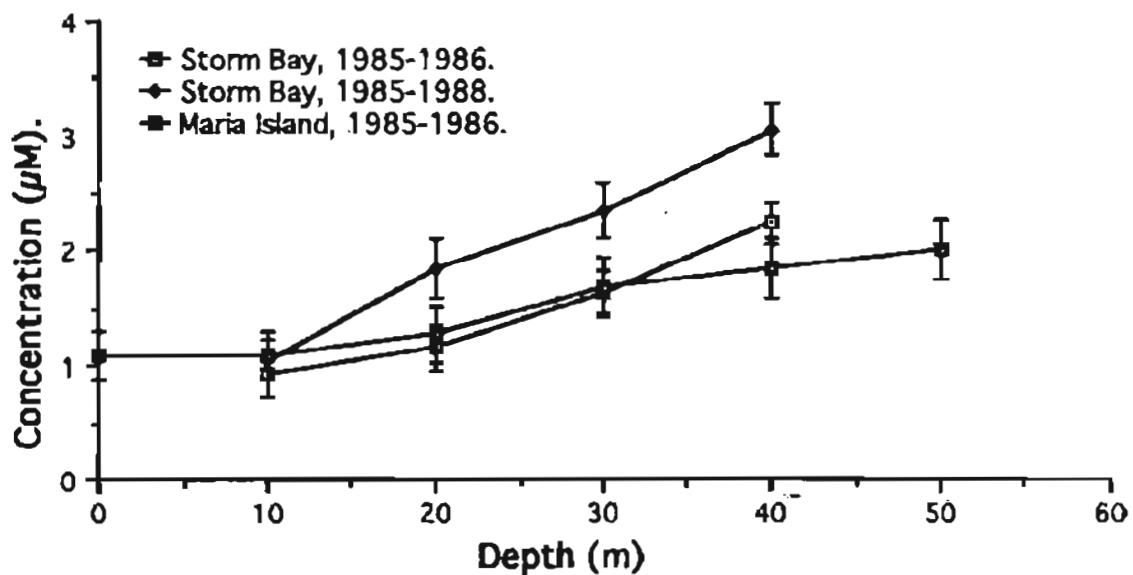
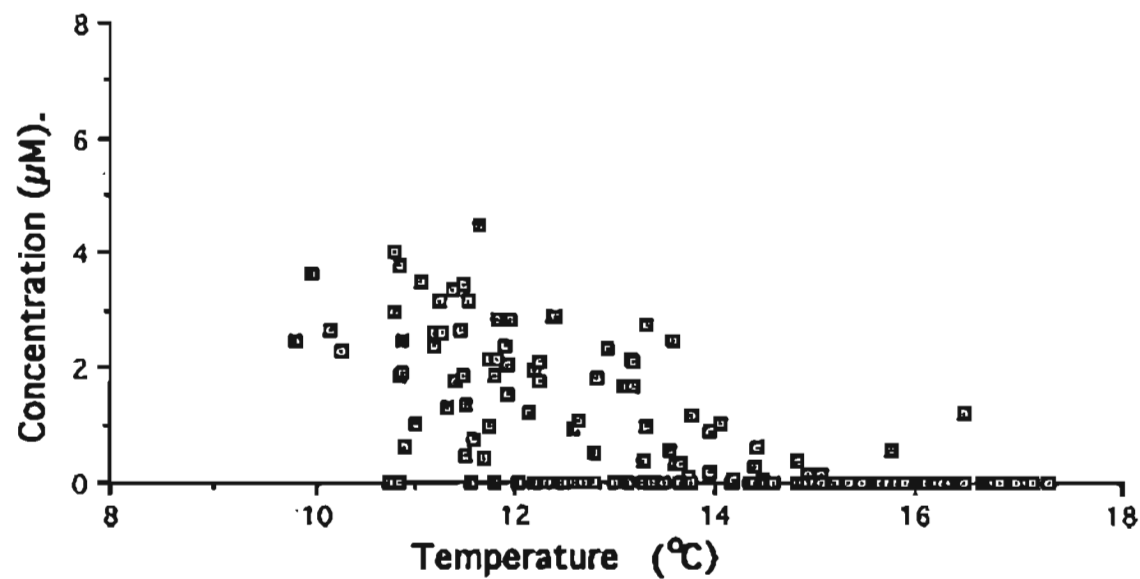
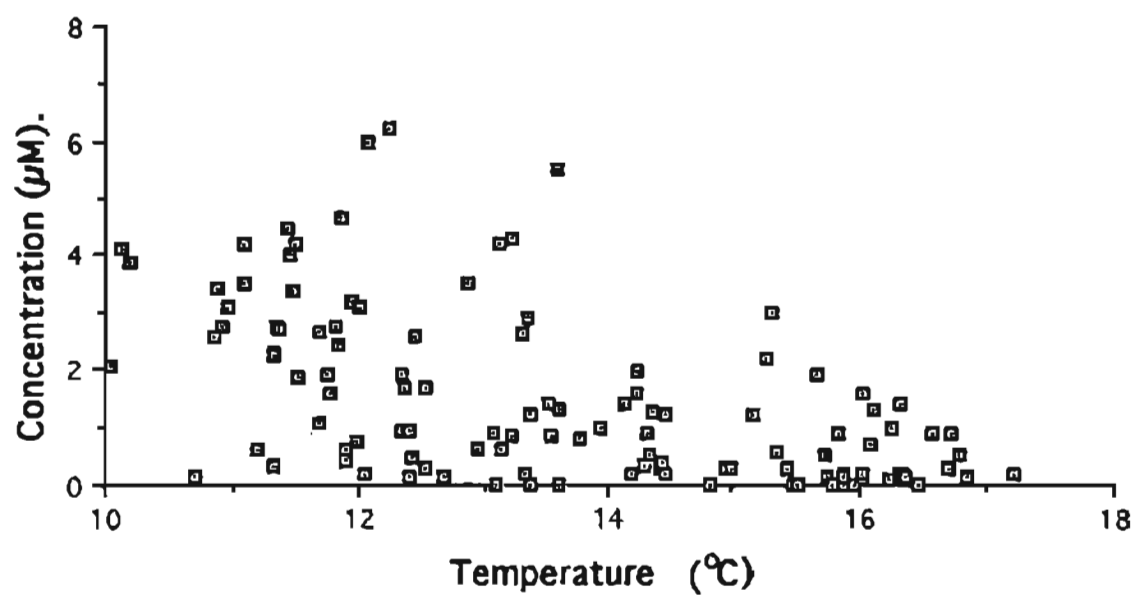


Fig. 2.18 Nitrate (nitrate+nitrite) concentration versus temperature at 10 m and 20 m depth from Storm Bay Data (1985-1988).

a) 10 m.

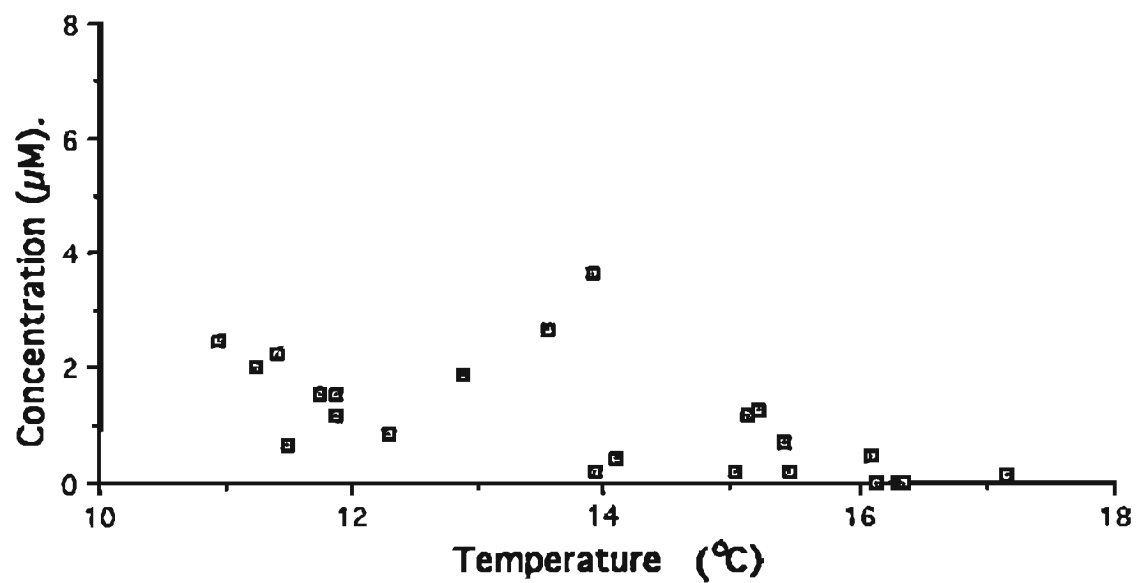


b) 20 m.

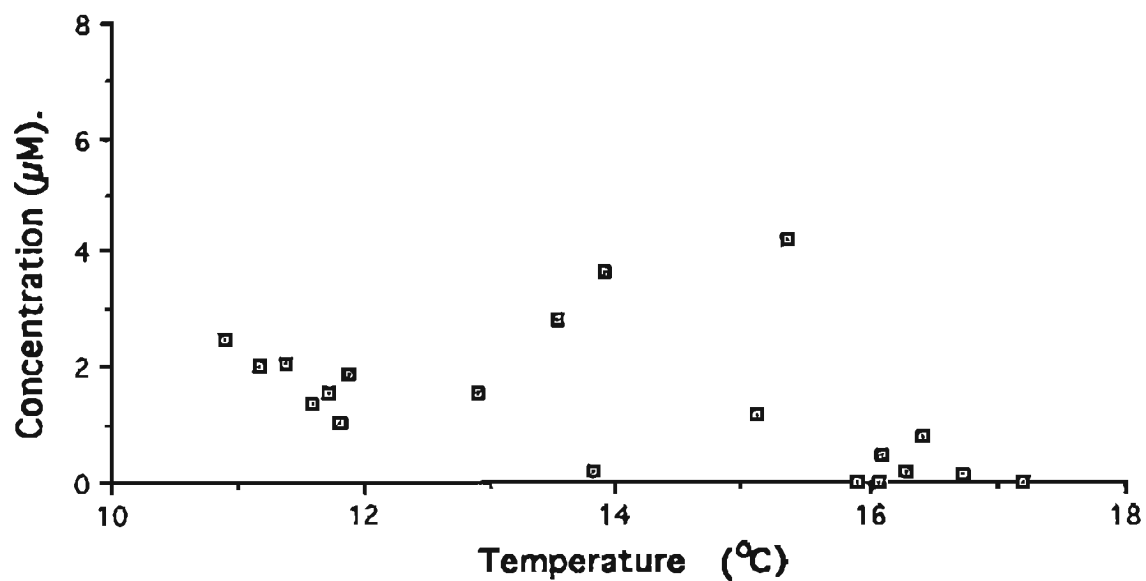


**Fig. 2.18** Nitrate (nitrate+nitrite) concentration versus temperature at 10 m and 20 m depth from Maria Is. data (1985-1986).

c) 10 m.



d) 20 m.



## PART 2, CHAPTER 3.

### ECKLONIA RADIATA

#### INTRODUCTION

The genus *Ecklonia* has a widespread distribution and there are a number of studies on its growth and productivity in various places of the world. These include studies on *E. cava* Kjellman communities in Japan (Yokohama *et al.* 1987; Hayashida 1977), *E. maxima* (Osbeck) Papenf. and *E. biruncinata* (Bory) Papenf. in S. Africa (Bolton and Anderson 1987) and *E. radiata* (C. Ag.) J. Agardh in New Zealand (Novaczek 1984 a, b & c). In Australia, the sole recognized species is *E. radiata* and studies have been conducted principally in Western Australia by Kirkman (1981 a & b, 1984 and 1989), Hatcher *et al.* (1987) and Wood (1987a). Other studies in Australia include those by Larkum (1986) in Port Jackson, New South Wales and Shepherd (1980) at Cape Northumberland, South Australia.

The thallus of *E. radiata* varies from 0.3-2 m high, arising from a hapteroid holdfast, with a single stipe bearing a complanate blade with distinct laterals. The stipe is terete, 2-100 cm long and 2-12mm in diameter. The blade, 25-120 cm long and 1.5-15 cm broad, grows from a basal meristem, with laterals rapidly developing from meristems at their bases. Laterals are often distichous and vary from 5-40 cm long and 1-10 cm broad (Womersley 1987). *E. radiata* is also found in South Africa and New Zealand.

Frond morphology in *E. radiata* is known to be very variable. In New Zealand, Lindauer (1961) recognized *E. radiata* forma *richardiana* (although expressing doubts as to the validity of the separate standing) to distinguish the type found in rough waters from that which develops in areas with

currents. In rough water types, laterals are denser (but fewer) and are themselves often lobed, and usually with numerous surface spines. In Tasmania, *E. radiata* is more often the smooth variety.

To distinguish between juvenile and mature plants Kirkman (1981) recognized three stages of development;

Stage 1, early sporophyte plants; their blades are entire and of oblong to linear shape, 6.5-27 cm.

Stage 2, plants show protuberances on the blade just above the stipe and the secondary blades are simple and entire, 19-34 cm.

Stage 3, plants have compound lateral blades emanating from the central lamina, 30-90 cm.

These distinctions are utilized in this study.

*Ecklonia radiata* is one of the most common macroalgae on the Tasmanian coastline. It can be found from intertidal rock pools down to depths of more than 30 m. The alga is found in areas moderately exposed to water motion, so that in sheltered sites it is found in relatively shallow waters exposed to wave action and in deeper waters influenced by currents, while in areas exposed to consistently large swells, it is found in deeper waters only (Sanderson and Thomas 1987; Edgar 1984).

The limit for distribution is set by the availability of suitable substrate and the clarity of water. Normally a rocky reef substrate suffices. In deeper more protected areas the alga is sometimes found attached to shells and small rocks overlying a sandy bottom.

At George III Reef, from 8-15 metres depth, the overall dominant plant cover is of red algae maintaining a dense lower storey of 10-30 cm in height. *E. radiata* is the most dominant of the brown algae. From 8-12m depth *E. radiata* plants are sparse but evenly distributed. From 12-15 m clumping of 20-50 individuals is not uncommon. Plants used for

monitoring were chosen on the basis of ease of location, proximity to other plant species investigated and were at 14 m depth.

Similarly at Bicheno, plants were chosen primarily on the basis of proximity to plants of other species investigated and ease of location underwater. The site chosen here was at a depth of 10 m. *E. radiata* occurred in approximately equal quantities with another furoid, *Phyllospora comosa*. Abundance of *E. radiata* plants at this depth ranged from 0 to more than 15/m<sup>2</sup>.

The decision to study this particular macroalga was taken also because of its ubiquity on the Tasmanian coastline and because of comparable research done on this species elsewhere. The aim was to determine the growth strategy and key environmental factors determining this strategy by monitoring growth parameters at two sites differing primarily in oceanic water types. Further information was hoped to be gained by reciprocal transplants to test the existence of possible ecotypes (see Part 2, Chapter 5).

## METHOD

### Growth measurement

As with other macroalgal species investigated in this study, methods for analysis of growth etc. were established at George III Reef before adopting them for plants at Bicheno.

Stage 3 (Kirkman 1981) plants were chosen for growth analysis and these occurred in the vicinity of the transect line at the 0 m mark in 14 m of water. Initially, fifteen plants were tagged and punched with a 5 mm diameter cork borer at 10 and 15 cm above the narrowest point below the stipe - meristem junction at the base of the blade. Individual plants were identified with a numbered plastic sheep-ear tag attached with a plastic electrical tie. At regular intervals, one month for the first year and two

months thereafter (mean; 57 days) plants were relocated, parameters measured and the blades repunched.

Parameters measured were stipe length, distance from the base of the meristem to the first punched hole, the distance between punched holes and distance from the second punched hole to the end of the blade. After the first year growth was confirmed as being confined to the first ten centimetres of the blade and from then on the blade was only punched once at a point 10 cm from the blade-stipe junction. An index of fertility was also formulated and assessed. Techniques utilized did not appear to have any adverse affects on the plants.

#### Measurement of Erosion

Growth of the blade of *Ecklonia radiata* has been likened to that of a moving conveyor belt of tissue, starting at the meristimatic region of the base and moving towards the end where it erodes. Erosion of the plants was calculated for each period as the growth increment of the plants (ie. the distance the first hole had moved down the lamina between sampling sessions) less the change in total length of the plant.

#### Fertility

The index of fertility was based on the area of blade covered by sori. Sori could be distinguished underwater as raised, lighter areas on the centre of the blade and at the base of laterals extending from the end of the lamina towards the meristem. The number of laterals from the end of the lamina to the extent of the sori (Fig. 3.1) was counted as well as the number of laterals covered by sori. This was conducted on the upper surface of the lamina only. These numbers constituted the index of reproductive status.

Periodically, more plants were tagged to make up for any lost due to old age, surge etc.

A similar sampling program was initiated at Bicheno (mean sampling interval; 61 days). Tagged plants were in the vicinity of other plant species monitored in 10 m of water.

### Annual Production

Values for production were obtained for comparison with values for *Ecklonia* beds obtained elsewhere. The method used followed that of Mann and Kirkman (1981). Mean annual production of Stage 3 plants was calculated as the product of the mean maximum lamina weight per unit length and the mean annual growth increment. This was converted to production per unit area of sea floor by multiplying by the mean density of plants.

Maximum lamina weight per unit length is likely to be seasonally variable (Larkum 1986) and so was assessed mid-summer and mid-winter at both sites. Ten to thirty stage three plants were collected in the immediate vicinity of monitored plants. Laminas were divided into either 5 or 10 cm sections from the base upwards and weighed. The combined results revealed the region of mean maximum weight per unit length.

Productivity per unit area was calculated 'overall' and for areas of 'continuous' cover of *E. radiata* at both sites. 'Overall' is defined as the total contribution of the plant to productivity in the area. 'Continuous' is in areas where *E. radiata* cover approaches 100%, in these areas contribution to productivity by *Ecklonia* is maximal.

Plant density was determined by recording the number of stage 3 plants within a metre square quadrat. Placement of the quadrats was determined by a diver using two sets of random numbers, 1-8 and 1-20. The first set corresponded to a compass direction and the second to a number of fin beats. The first quadrat was taken from where it landed when thrown from the boat and the numbers were used for subsequent quadrats. Overall



cover was obtained from directly where the quadrat landed at the final fin beat, the quadrat was then relocated to the closest area of continuous cover for a second reading.

At both sites density measurements were confined to depths similar to that of the monitored plants. Twenty quadrats were used for analyses of continuous and overall densities at Bicheno and continuous density at George III Reef.

An alternative method was used for the overall rating at George III Reef. Due to the sparse distribution of plants there, overall density of plants was determined from strip transects. Two x one hundred metre transects were laid at right angles and the number of stage 3 plants within two metres each side of the line in 20 metre sections was counted (ten 20 x 2 m quadrats).

### Statistics

Stepwise multiple linear regression analysis was used to develop models relating variations in growth rates to measured environmental parameters. This was done for George III Reef plants only. Stepwise multiple regression analysis regresses in an exploratory manner a variable Y on variables X1, X2, X3, . . . ., taking various combinations of these to obtain a minimum of unexplained residual variance in terms of the smallest number of independent variables by dropping any potential independent variables that do not remove a significant independent portion of the variation (Sokal and Rohlf 1969). Tests of significance were calculated taking into consideration the number of candidate predictors (Wilkinson and Dallal 1981). Variables as detailed in Part 2, Chapter 2, 'The Coastal Environment', were used for regressions.

Variables chosen for analysis were;

1. CSIRO values that were most highly correlated with measured values (TEMP20, NIT10, NIT20 and PO420 where '20' refers to 20 m and '10' to 10 m depth).
2. sea state (CSTATE, AVSWELL-average swell and ADJSWELL-adjusted swell value for George III Reef) and
3. daily sunshine (SUNSHG-daily sunshine at Grove, hrs/day), available from the Bureau of Meteorology.

(or eight candidate predictors).

Variables most likely to affect growth rates of Bicheno plants were regressed individually refers to temperatures taken on site.

As the majority of plants were the same between sampling sessions at both sites, data was checked for serial correlation using the Durbin-Watson statistic.

Statistical packages; Excel (Microsoft Corp.), Statview 512+ (Brainpower Inc.) and Systat (Systat Inc.) were used in calculation of standard errors, linear and nonlinear regressions. Unless mentioned otherwise all errors and error bars are standard error.

## RESULTS

### Growth Increment

Growth increment of *E. radiata* at George III Reef and Bicheno is depicted in Figs 3.2. These demonstrate a strong seasonality to growth at both sites. At George III Reef over the period of four years, there are obvious maxima in November-December and minima in June-July. The situation at Bicheno is not quite as simple with a peak spanning October to January with a minimum in March. Average growth increment between sessions at George III Reef was  $2.1 \pm 0.2$  mm/day ( $n=26$ ) and at Bicheno;  $2.0 \pm 0.2$

mm/day (n=8), for the period of the study. Annual growth increment for George III Reef was  $2.19 \pm 0.09$  mm/day (n=4) and at Bicheno; 1.96 mm/day.

Stepwise regression of *Ecklonia* increment against measured environmental parameters, indicates light, temperature and average swell to be the predominant factors affecting growth increment at George III Reef (partial prob.=.0001, .0002, .0089 respectively). Growth increment may be represented by the following equation:

$$\text{Growth increment (mm/day)} = 0.685 + 0.065 \times \text{SUNSHG} - 0.037 \times \text{TEMP20} - 0.118 \times \text{AVSWELL}, \text{ where } r = 0.883 \text{ and } p = .0001.$$

If the number of candidate predictors is taken into account (according to Wilkinson and Dallal 1981) then the confidence interval of this best fit equation is reduced to  $p = .01$ .

At Bicheno of the possible environmental factors, light demonstrates the best correlation with growth of *Ecklonia*. The equation representing growth increment is:

$$\text{Growth increment (mm/day)} = -0.016 + 0.035 \times \text{SUNSHB} \quad r = .727 \quad p = .017$$

#### Mean lamina length and erosion

Changes in mean lamina length and rate of erosion are shown in Figs 3.3 and 3.4. At George III Reef, rates of erosion are at their greatest over summer. Mean lamina length increases regularly during mid-late summer with a decrease from February to June indicating that the rates of erosion exceed growth increment February to June while in early summer, despite relatively high rates of erosion, growth rates exceed the rate of erosion. Levels of standing stock of *E. radiata* must consequently be highest in January-February.

Regression of rates of erosion indicate average nitrate concentration over the sampling periods as being the predominant influencing factor. Erosion may be represented by the equation.

$$\text{Erosion rate (mm/day)} = 0.275 - 0.075 \times \text{NTT10}, r=0.717 \quad p = .0003$$

If the number of candidate predictors is taken into account (according to Wilkinson and Dallal 1981) then the confidence interval of this best fit equation is reduced to  $p = .05$ .

Temperature and phosphate concentrations also demonstrate strong correlations with rates of erosion ( $r=.664 \quad p=.0014$ ,  $r=.631 \quad p=.0028$  respectively). This implies an increase in erosion as the sea-water warms and nutrients decline. Separating individual factors as being directly responsible for erosion is tenuous.

At Bicheno rates of erosion exceeding growth rate were maintained throughout most of 1988, resulting in a halving of the average length of the lamina of the plants examined over the period of the study. This would appear to have resulted from adverse conditions and may be due either to warmer water temperatures experienced and consequent near zero nitrate concentrations experienced early that year under the influence of the EAC and the warm winter of 1988 or greater exposure to wave action and thus more scour as a result of the disappearance of *Macrocystis* from the area in 1988. The *Macrocystis* forests previously in the vicinity possibly served to dampen the effects of swell. Annual mean length of the lamina of monitored plants at George III Reef is  $78.2 \pm 1.8$  cm while at Bicheno  $54.5 \pm 5.6$  cm.

For Bicheno, no nitrate analyses are available, however average sea-state is correlated and is best represented by the equation;

Erosion (mm/day)

$$= -0.746 + 0.358 \times \text{CSTATE}; r = 0.73, p = .017$$

If one point is excluded (corresponding to April, 1988), there is also a strong relationship with temperature which may be represented;

$$= -0.29 + 0.04 \times \text{TEMPME}, r = .899, p = 0.001$$

### Stipe length

Stipe length of a number of plants from both sites are depicted in Figure 3.5. Stipe lengths of plants at George III Reef show little variation between plants and over time with a minimum of 4.0 cm and a maximum of 13.5 cm. At Bicheno plant stipe lengths also show little variation over time and there is a variety of sizes ranging from 5.5 to 35.5 cm. Overall stipe length of monitored plants at George III Reef is  $8.3 \pm 0.1$  cm and  $11.0 \pm 0.5$  cm at Bicheno.

### Depletion curves

Natural log of plant loss for George III Reef and Bicheno plants (see Fig. 3.6) results in a near linear relationship. This differs from a 'survivorship' curve as the plants are of unknown age and is termed a 'depletion' curve. Depletion curves are likely to give a more inflated estimate of the lifespan as the plants as observations begin with a set of proven survivors (Harper 1971, Silvertown 1982). These indicate half lives of 23 months for George III Reef plants and 10 months for the Bicheno plants.

While the relationship for these plants is based solely on 15 plants, indicating small confidence, the closeness to linearity and the similar findings for the *Phyllospora* plants (chapter 6) i.e. that of a greater rate of

mortality for the Bicheno plants than the George III Reef is effectively supported.

### Fertility Index

Fertility Index for George III Reef indicates a maximum in the winter months and a minimum in late summer (Fig. 3.7). The index for the Bicheno plants decreased overall throughout the period of sampling, this may be attributed to the altered environment of these plants as a result of the disappearance of the protective *Macrocystis* forest or the effect of the EAC in the summer and the warmer winter (than the previous 2-4 years) of 1988.

### Harvested plants

Figure 3.8 relates to the harvesting of plants in summer and winter at both sites. The method for measuring productivity as expressed by Mann and Kirkman (1981) relies on a plateauing of the maximal biomass region along the length of the frond. Examination of the graphs demonstrates no obvious plateau in the plants from either George III Reef or Bicheno, rather a peaking of biomass at a point 15-30 cm from the stipe-meristem junction. This is in agreement with Larkum (1986) for plants at Fairlight Bay in NSW. For the purposes of this study, maximal biomass is taken as being equivalent to this peak and individual plant annual productivity is taken as the product of the mean of the two maximal biomass values and the mean annual length increment.

The weight per segment of lamina of George III Reef plants (Fig. 3.8) shows a considerable difference between summer and winter. The section of maximal biomass occurs further along the frond, at 20-25 cm, in summer than winter, at 10-15 cm, and is less, at  $17 (\pm 2)$  gm/5cm ( $n=10$ ) than the winter value of  $29 (\pm 2)$  gm/5cm ( $n=16$ ) (overall average maximum;  $4.6 \pm 0.4$

gm/cm, n=20) . There is no definite pattern at Bicheno, with a maximal weight per length of  $35 \pm 5$  gm / 5 cm (n=11) at 10-15 cm in the summer and  $39 \pm 4$  gm/5 cm (n=18) at 25-30 cm in the winter (with an overall average maximum of  $7.4 \pm 0.7$  gm/cm, n=22).

### Annual Productivity

Tables 3.1-3.2 show the details for calculation of production per individual plant and per unit area. This is calculated for overall cover and for areas of continuous cover.

**Table 3.1** Details of density determinations. Plants per square metre in areas of overall and continuous cover at both sites. 'N' is the number of quadrats used in the estimation.

	<u>Overall cover</u>			<u>Continuous cover</u>		
	No. Plants	S.E.	N.	No. Plants	S.E.	N.
George III Reef	0.7	0.1	10	5.0	0.4	20
Bicheno	3.9	0.6	20	8.8	0.5	20

**Table 3.2.** Estimation of annual productivity for the period investigated of *Ecklonia radiata* at the two sites for overall and for continuous cover. Calculated as the product of the growth increment, maximum biomass per lamina unit length and plant densities (see Table 3.1).

	Growth Increment (mm/day)	Max. Lamina Biomass (gm/cm)	Productivity /plant (kg)	Overall Productivity per m <sup>2</sup> (kg)	Maximum productivity per m <sup>2</sup> (kg)
George III Reef	2.19 $\pm 0.09$	4.6 $\pm 0.4$	0.36 $\pm 0.03$	0.25 $\pm 0.04$	1.8 $\pm 0.2$
Bicheno	1.96	7.4	0.53	2.1	4.7

Despite the fact that plants at Bicheno were shorter than at George III Reef, on an individual basis, they were more productive and potentially more productive on a community basis than at George III Reef. This is probably due at least in part to the shallower depth at Bicheno, thus more light is available and a greater density of plants possible.

## DISCUSSION

### Growth rates

The predicted light climate (see Chapter 2; The Coastal Environment) for both sites indicates average daily levels of less than 100  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at the level of the algae. If it is assumed that saturating levels for *Ecklonia* fall in the range for a mid-sublittoral species, corresponding to 150-250  $\mu\text{mol m}^{-2}\text{s}^{-1}$  (Lüning 1981), then these algae would appear to be light limited for much of the year at both sites. This agrees with the principal factor determining growth rates as being light .

While neither temperature nor nitrate concentration is implicated in affecting the growth of the alga at George III Reef, if values for growth increment are deleted that correspond to average water temperatures of over 14.5°C and thus to waters very low in nitrogen (see Figs 2.21 and 2.22), the regression of growth increment against average daily sunshine at George III Reef is improved ( $r = 0.53$ ,  $p = 0.0005$  to  $r=0.91$ ,  $p=.0001$  see Fig. 3.9). Lower measured growth rates at temperatures greater than 14.5°C may thus be due to the higher temperatures or to limiting levels of available nitrate at those temperatures.

Deysher and Dean (1986) found a similar relationship in their studies on recruitment success of *Macrocystis* sporophytes. Laboratory studies of sporophyte initiation from *Macrocystis* gametophytes demonstrated temperature had little affect over 16°C. In the field however as temperatures exceeded 16°C recruitment success decreased. This was attributed to low levels of nutrients in particular nitrogen. Fertilization with slow release nutrients (nitrogen and phosphorous) enhanced recruitment success at the higher temperatures.



The third factor; swell, may influence growth indirectly through light limitation. Increase in swell can increase the amount of suspended matter in the water column in coastal areas. This is especially true around George III Reef where there is much shallow water. The suspended matter in the water column, decreases the light attenuation and thus the amount of light reaching the algae. It is unlikely that the swell in itself would affect the growth rate in a negative manner; in fact water motion up to certain levels has been found to be beneficial (Lobban *et al.* 1985).

At Bicheno, deleting values corresponding to high average temperature values ( $>15^{\circ}\text{C}$ .) does not increase the significance of the relationship although the correlation coefficient is improved ( $r = .741$ ,  $p = .014$  to  $r = .933$ ,  $p = .014$ ).

Growth of *Ecklonia radiata* off the Western Australian coast, has been negatively correlated with ambient sea temperatures (ie. not nitrates) when these are above  $20^{\circ}\text{C}$  (Hatcher *et al.* 1987; Kirkman 1981). As temperatures rarely get above  $18^{\circ}\text{C}$  at George III Reef or Bicheno, nitrate depletion from the water column, particularly in late summer would appear to be the factor determining *Ecklonia's* growth in this instance. Pre-conditioning of the plants in Tasmania to cooler waters and consequent temperature stress at lower temperatures relative to the Western Australian plants cannot be dismissed however.

#### Rates of Erosion

The difference in factors influencing erosion between the two sites may be explained in terms of the situation of the plants (temperature and nutrients at George III Reef, but temperature and sea state at Bicheno). The *Ecklonia* site at Bicheno is subject to comparatively stronger surge action due to the shallower habitat and the aspect of the substrate (into the

predominant sea and swell direction). This would result in abrasion from the surrounding substrate and possibly from neighbouring algae, as the *Ecklonia* is moved to and fro by the action of swell. The *Ecklonia* at George III Reef is not subject to as great a swell action as it is deeper and is on comparatively flat bottom. There are also few other macroalgae other than small reds in close proximity.

### Lifespan

Lifespan of George III Reef plants appears to be nearly twice that of Bicheno plants. This may be due to the relatively sheltered waters at George III Reef in 15 m of water. Plants at Bicheno are shallower and in a more dynamic environment. Warmer waters at Bicheno may also contribute to more rapidly maturing plants at this site.

On at least two occasions, plants at George III Reef developed a die-back of the tissue in the vicinity of the meristem. This gradually spread to include most of the basal meristematic tissue. In plants so affected, growth rate slowed to near zero and the plants eventually disappeared. Time from inception to disappearance of the plant was in the vicinity of 3-6 months. Cause of the 'rot' could have been either disease or natural senescence.

### Fertility

The index of fertility gives an indication of the total area of the blade covered by sori. This peaks in winter at George III Reef. Comparison with Bicheno results, where fertility shows a decline over the entire period, are tenuous as there appear to be factors not accounted for affecting the results at Bicheno, viz. loss of the surrounding *Macrocystis* and thus its buffering effect against swell action.

The area occupied by the sori does not necessarily give an indication of actual number of spores released but just the potential for reproduction. Joska & Bolton (1987) found with *Ecklonia maxima* in South Africa that not only the amount of fertile area varied with season, but so did spore release per unit fertile area. There, sorus area peaked in early Spring and the number of spores released from sorus tissue per cm<sup>2</sup> peaked two-three months afterwards. If the situation here was comparable, then spore release is likely to peak in early spring. This agrees with a perception of optimal growth strategy of the plants. Juveniles developing in the months after spore release would be exposed to more favourable conditions available in the spring months.

#### Studies elsewhere

Comparison of growth parameters with those from other studies on *Ecklonia radiata* reveal strong correlations (summarized in table 3.3, p. 114) that may aid in interpreting overall growth determining factors. Mean annual lamina length against annual increment demonstrates a strong relationship for a quadratic equation ( $r=0.97$ ,  $p=.0001$ ). This includes data from the longer stiped New Zealand form of *E. radiata*. (See Fig. 3.10 a), thus indicating a consistency within the species over a wide geographical range.

Mean length of the lamina shows a strong correlation with depth of the plants, if the New Zealand plants (long stipes) and the Abrolhos Is plants (at the limit of geographical distribution) are excluded (Fig. 3.10 b). There is a rise in the length of the lamina with depth to 15 m. This may be a response to exposure to swell action and 15 m corresponds to where the effect of swell is minimal on the length of the lamina of the plants. This in agreement with the correlation results above, where erosion of the Bicheno plants in 10 m of water appeared to be affected by sea-state.

The erosion of the plants at 15 m at George III Reef appeared to be most closely related to temperature and nutrient concentration of the water.

Abrolhos Is plants are close to the northern limit of distribution for *E. radiata* and these plants may be expected to show deviations from the norm. The New Zealand plants appear to be exceptions due to the longer stipes on these individuals. The increased stipe length may expose the plants to more water motion and resultant abrasion. The longer stipes plants may also represent a differing subspecies of *Ecklonia radiata* that erodes more quickly.

A plot of individual plant productivity against depth (Fig. 3.10 c) shows no apparent relationship indicating available light may not be limiting to annual production (although light has a large effect on rates at given times during the year). Productivity per unit area however is negatively correlated with depth (Fig. 3.10 d).

Individual plant productivity may be better explained by temperature. A strong relationship is found if the product of biomass per unit length and increment is plotted against mean annual temperature if the Abrolhos Islands plants are not included ( $r=.975$ ,  $p=.0048$ , Fig. 3.10 e). This again is probably caused by the fact that *Ecklonia* is at its northernmost limit here. From these results it would appear that as annual average temperatures from at least 13.5°C to 20.3°C increase, individual plant productivity of *Ecklonia* increases, above which there is a rapid decrease.

As it is generally considered that nutrients in the form of nitrates are less available further north in warmer waters (Rochford 1984, Jitts 1965), then average annual temperatures must be increasing the rate of growth of the *Ecklonia* from 13.5°C to 20.3°C, over and above the effect of reduced nitrate concentrations. The reduction in growth above 20.3°C may be attributable to lethal temperatures for normal plant processes but extended nutrient depletion as a cause cannot be ruled out.

Other values for *Ecklonia* productivity, (wet weight) include Kirkman (1981); 20.7 kg/m<sup>2</sup>/yr off Perth, Western Australia in 2-5 m of water, 16.6 kg/m<sup>2</sup>/yr by Larkum (1986) in Fairlight Bay, N.S.W. in 1.5 m of water and Novacek (1984b) in Goat Island Bay in New Zealand (using a very different method) of 34 kg/m<sup>2</sup>/yr in 7 m of water. For *E. cava* in Japan Yokohama *et al.* (1987) found 17 kg/m<sup>2</sup>/yr at 5 m depth. The lower values of 4.7 kg/m<sup>2</sup>/yr at Bicheno and 1.8 kg/m<sup>2</sup>/yr at George III Reef in found in this study are likely to be related to the greater depth of the plants.

## SUMMARY

Light appears to be the most significant factor affecting the rate of increase in lamina length and thus production at Bicheno and George III Reef. At George III Reef, temperature and to a lesser extent swell also affect growth rates. Swell may be acting indirectly through its affect on light transmittance.

A regression of light against growth is improved at both sites if values are deleted where the average water temperature is above 14.5°C. The negative effect of temperature may be due to nitrate depletion.

Rates of erosion of the blade at George III Reef are most closely related to temperature and negatively to the nitrate content of the water. At Bicheno, rates of erosion are affected by sea-state and temperature. The effect of sea state may be as a result of abrasion caused by water motion. This factor is not evident at George III Reef due to the greater depth of the algae studied and the lower incidence of high swell action there.

George III Reef *Ecklonia* has a reproductive maximum in late winter-early spring, ensuring optimal conditions for following juveniles.

Half lives from depletion curves are 23 months for George III Reef plants and 10 months for the Bicheno plants.

Calculation of annual productivity at both sites for *Ecklonia* indicates for overall and areas of continuous cover values of 0.25 and 1.8 kg (wet weight)/m<sup>2</sup>/yr for George III Reef and 2.1 and 4.7 kg (wet weight)/m<sup>2</sup>/yr at Bicheno.

Comparison of plant characteristics in this study with plants from other studies in Australia and New Zealand, reveals strong trends between different populations indicating a consistency within the species over a wide geographical range.

Individual plant productivity is positively correlated with temperature from 13.5°C to 20.3°C . Plants at the Abrolhos Is, W.A. where the mean annual temperature is 22.3°C , are less productive and this area also corresponds to the northernmost limit of the alga. Due to the close relationship of temperature to nitrate concentration, the cause of the drop in productivity of *Ecklonia* in waters with a mean annual temperature over 20.3°C is uncertain.

**Table 3.3** Summary of results of studies on *Ecklonia radiata*. Confidence intervals (95%) are given and the number of plants or quadrats assessed (in brackets) where given.

Who	Where	Exposure to Wave Action.	Temp. Range °C.	Depth (m)	Av. Lamina Length (cm)	Av. Lamina Incre (mm/day)	Stipe Length (cm)	Lamina Biomass (g/cm)	Plant Density (No./m)	Half-Life (days)
This Study	G III Reef	Mod	11-17	14	78 ±3.1 (26)	2.1 ±0.2 (26)	8.29 ±0.09 (26)	4.6 ±0.4 (20)	0.7 ±0.1 (10)	690
	Bicheno	Mod	12-20	10	54 ±11 (8)	2.0 ±0.2 (8)	11.02 ±1.01 (8)	7.4 ±1.8 (22)	3.9 ±0.6 (3.9)	300
	Hatcher et. al. 1987	Mod+	19-25	4.5	38.1 ±4.8 (165)	1.28 ±.15 (165)	5.66 ±.75 (30)	11.6 ±1.7 (30)	0.62 (1)	272
	Abrolhos L.	Mod+	"	7	25.7 ±4.9 (131)	.75 ±.11 (131)	4.57 ±.87 (30)	10.9 ±2.8 (30)	.06 ±3.2 (20)	290
Kirkman 1981	Marmion	Mod	15-25	2-5	49.9 ±2.7 (1449)	1.78 ±.16 (2911)	7.37 ±1.42 (1449)	11.0 ±.7 (1449)	24.5 ±3.3 (20)	?
	Marmion	Mod	"	10	56.9 ±4.1 (60)	1.72 ±.35 (353)	7.26 ±.72 (45)	11.8 ±1.2 (60)	11.8 ±3.2 (20)	?
	Five Fathom Reef	Mod+	?	21	74.1 ±12.5 (167)	2.62 ±.51 (167)	10.1 ±3.32 (183)	7.49 ±1.4 (167)	.56 ±.1 (20)	?
Larkum 1986	Fairlight Bay	Sheltered	?	1.5	33.8 ±7.1 (270)	1.29 ±.37 (270)	8.9 ±.75 (270)	13.5 ±1.8 (270)	22.5 ±3 (10)	?
Shepherd 1980	Cape Northumberland	Mod+	12-17	12-15	71.57 ±5.56 (102)	2.05 ±.21 (102)	11.73 ±.562 (102)	? (102)	? (102)	326
Novaczek 1984 a, b	Goat Is	Sheltered	17.5	7		.524	106	47		1401
	Bay, N.Z.	Mod	22	15		.494	65	16		
							±2.2			951

Fig. 3.1 Diagram of showing the typical distribution of sori over the surface of the lamina of *Ecklonia radiata*. The fertility index was based on the extent of coverage. The measure was the number of laterals from the end of the lamina it extended. In this instance it would be 10:9 (10 for the extent down the central lamina and 9 for the number of laterals covered).

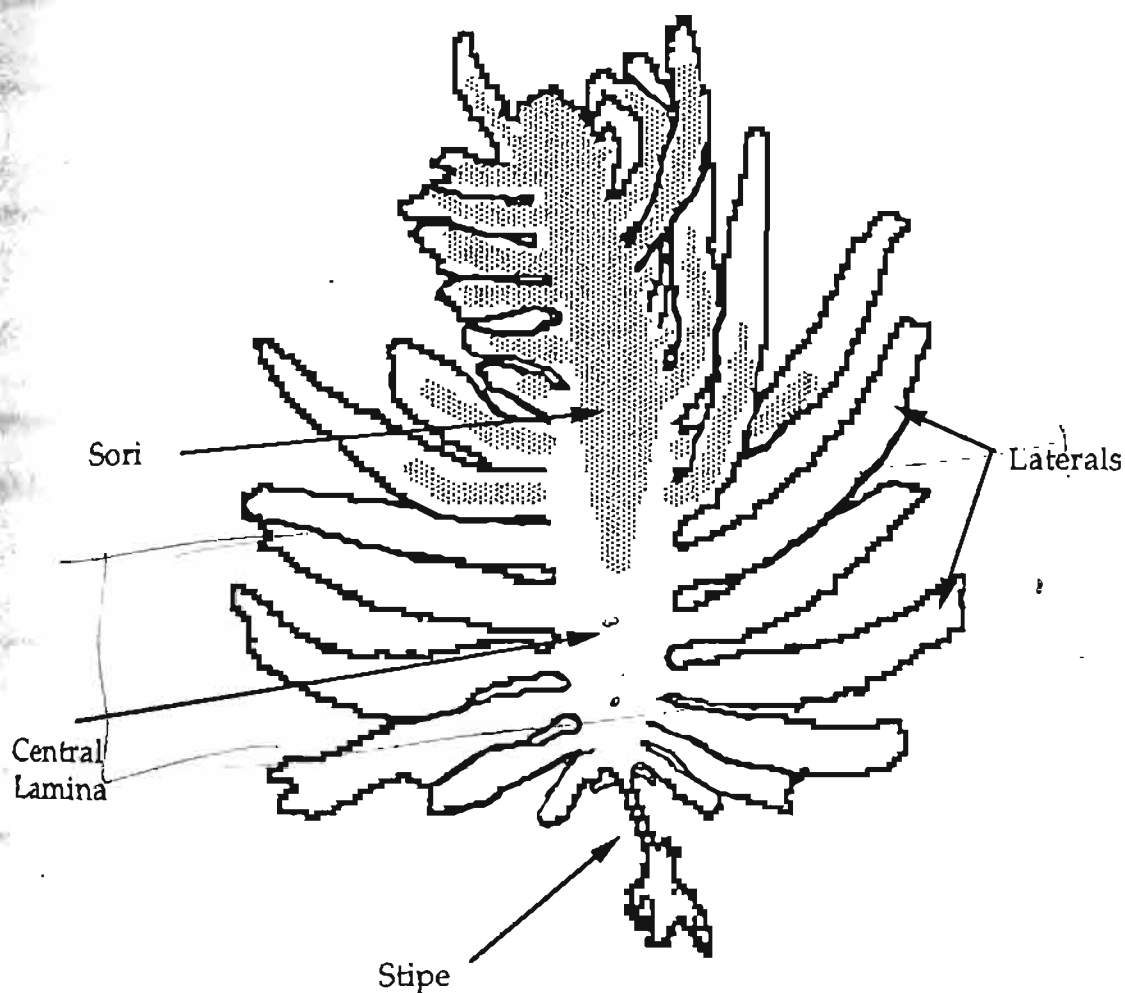
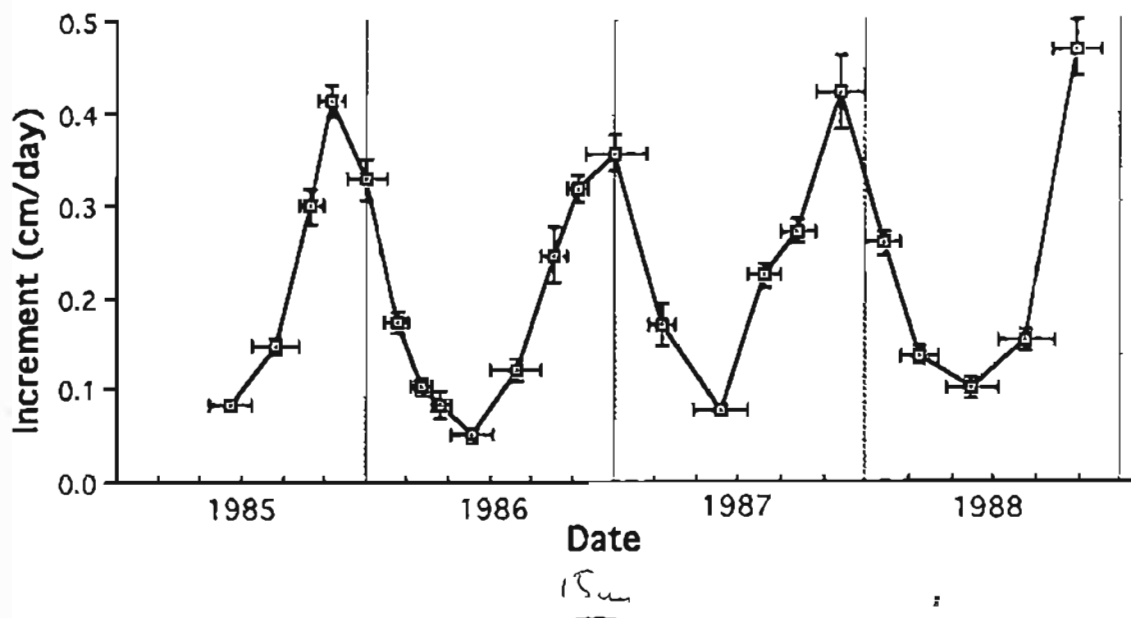




Fig. 3.2 Rate of increase in lamina length. Vertical bars are standard error and horizontal are the sample period.

a) George III Reef



b) Bicheno

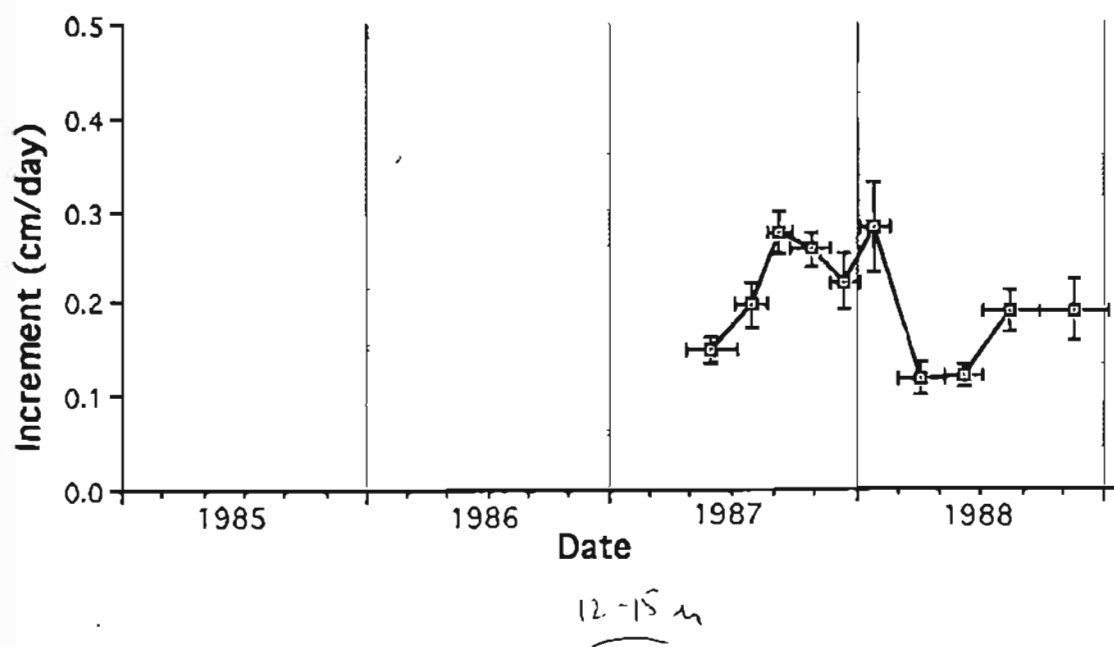
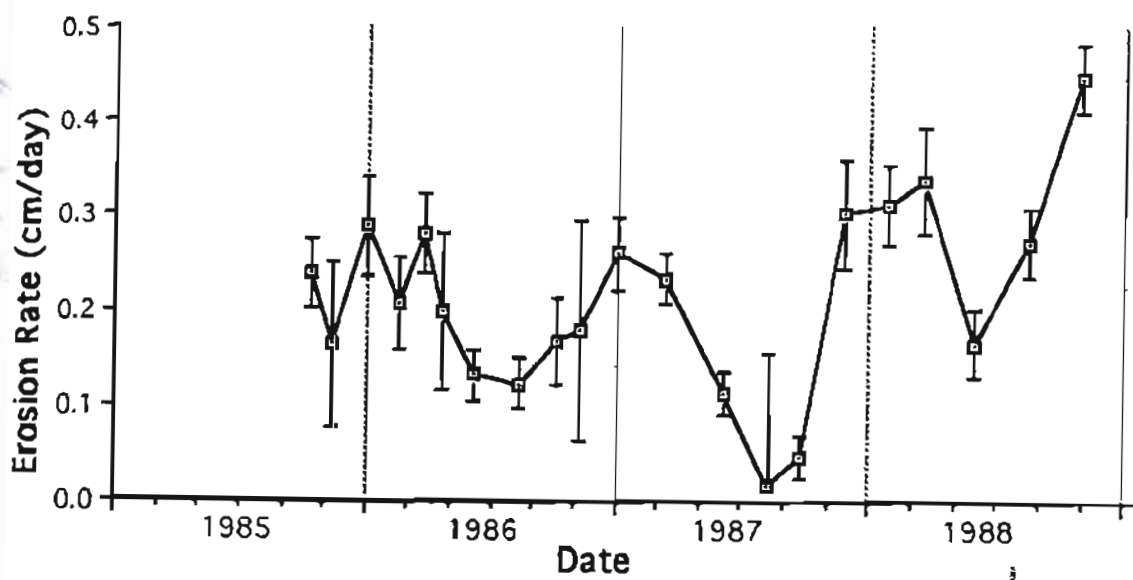


Fig. 3.4 Erosion rate of the lamina blade.

a) George III Reef.



b) Bicheno

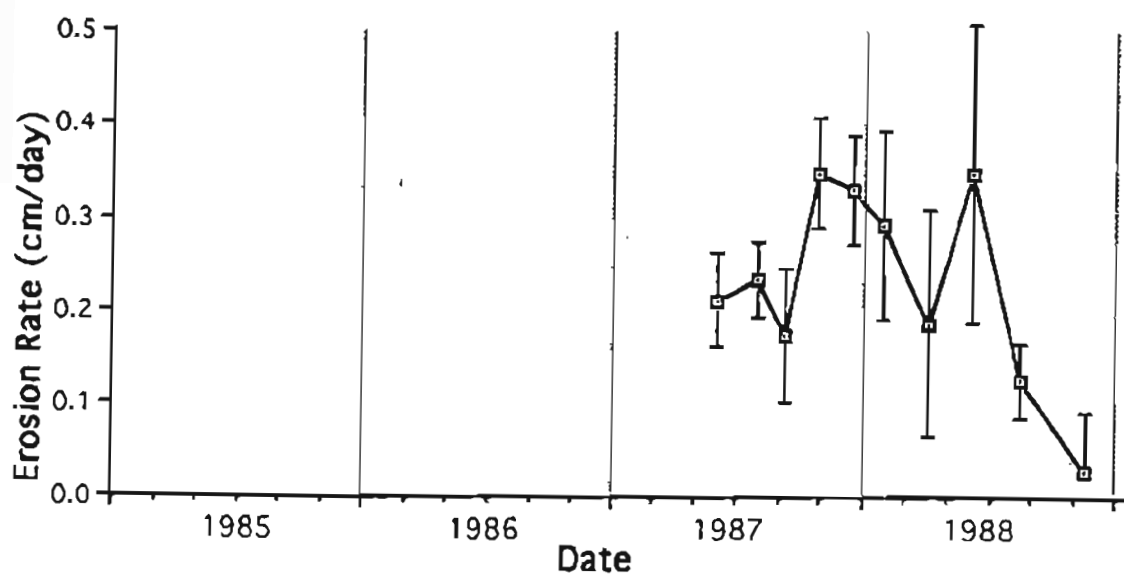
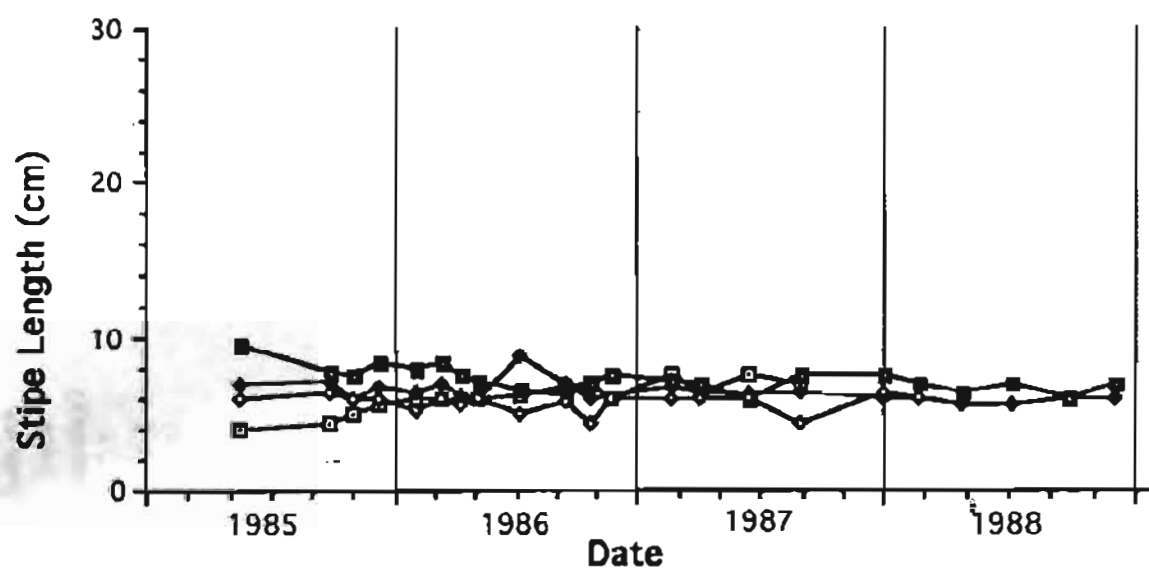
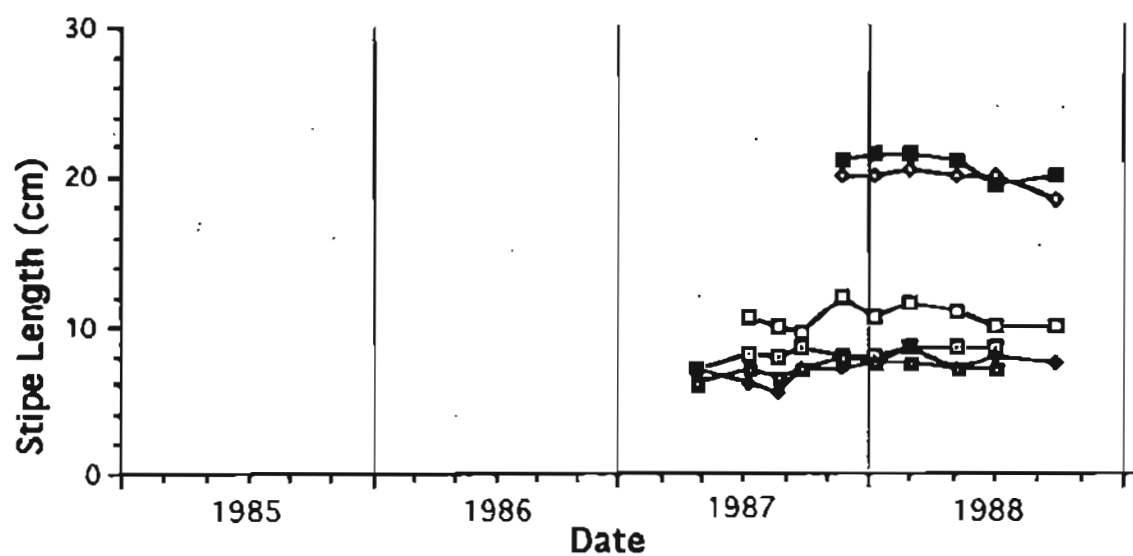


Fig. 3.5 Plot of change in length of stipes for some of the longer term-monitored individuals at both sites.

a) George III Reef.

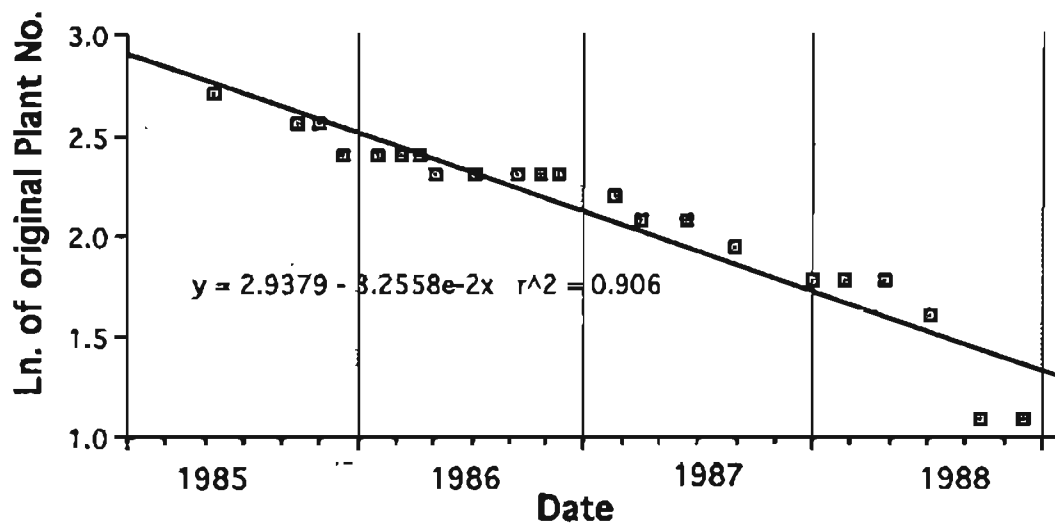


b) Bicheno



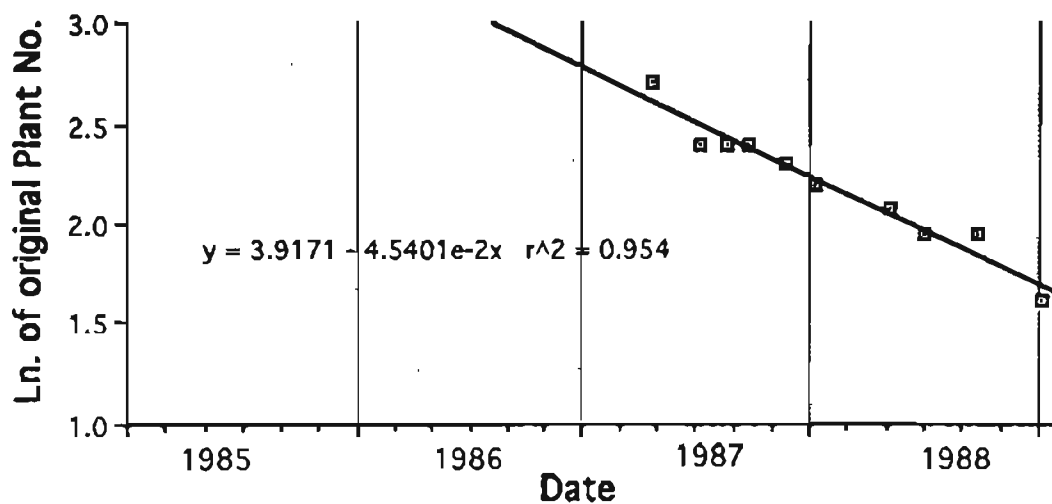
**Fig. 3.6** Natural log. of number of original tagged plants versus time for both sites or 'depletion curves'.

**a) George III Reef.**



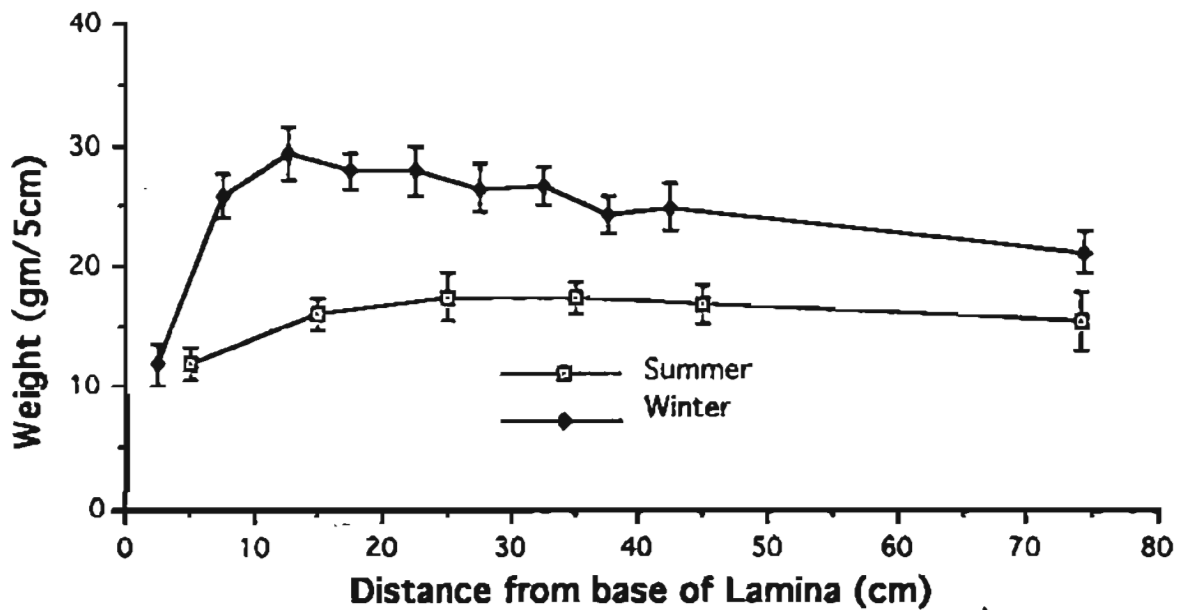
15

**b) Bicheno**



**Fig. 3.8** Mean biomass variation over the extent of the lamina for summer and winter (5 cm segments from the base of the meristem).

**a) George III Reef**



**b) Bicheno**

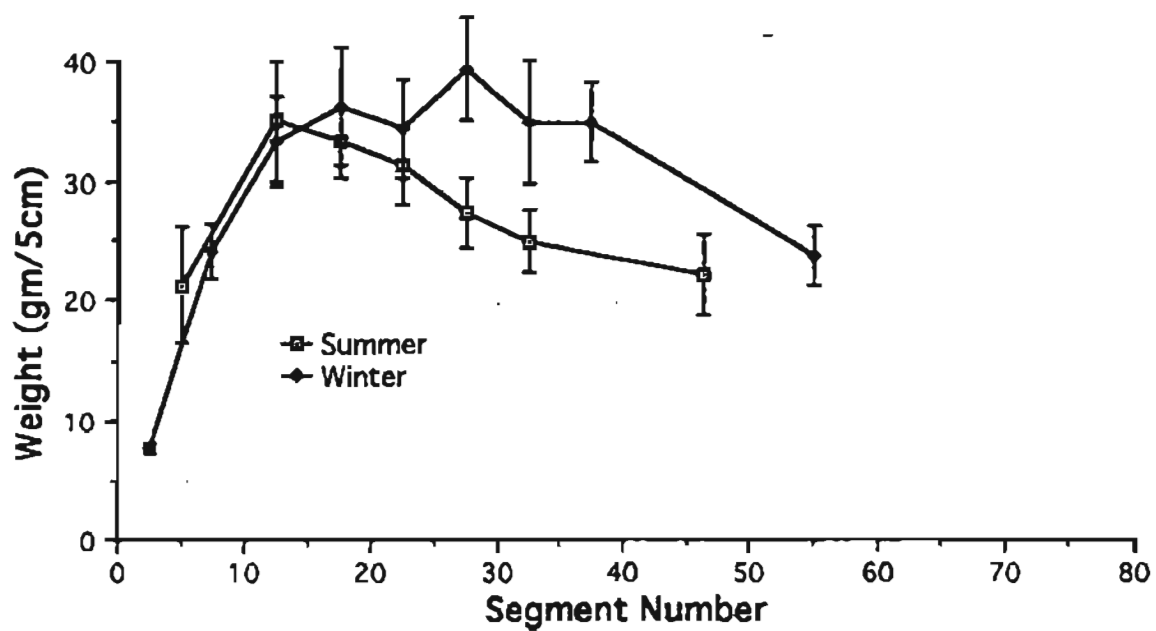
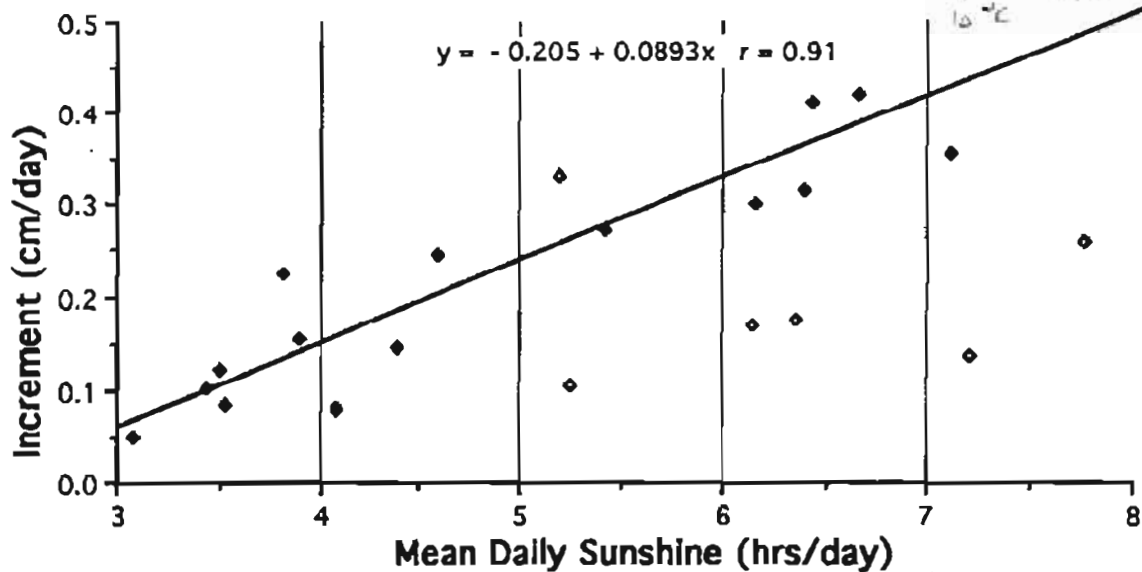
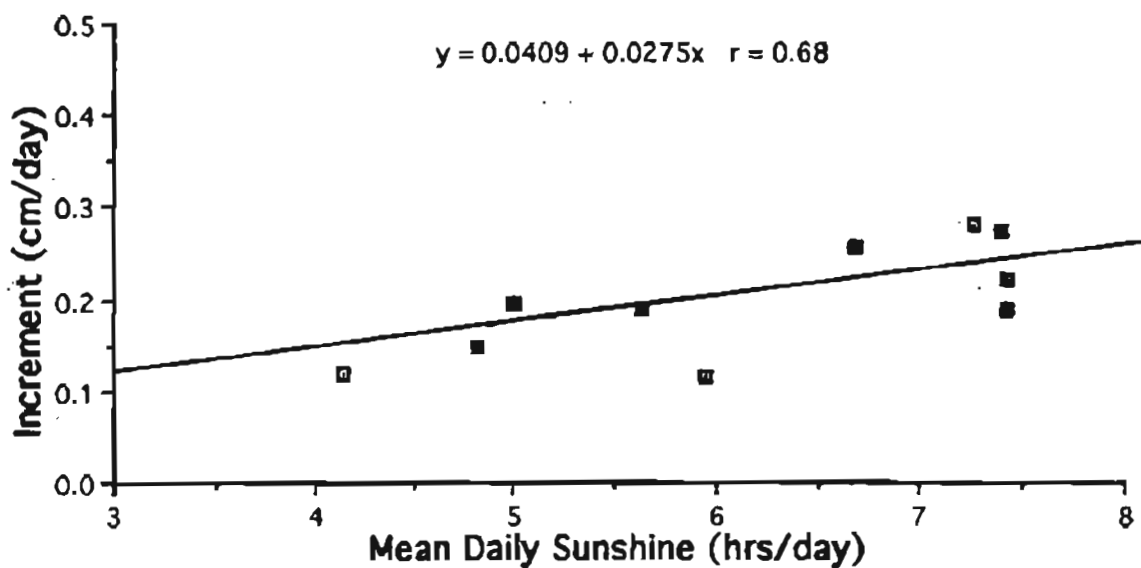


Fig 3.9 Graph of growth increment versus mean daily sunshine. Open points are those that correspond to periods where the mean ambient temperature was greater than 15°C.

a) George III Reef

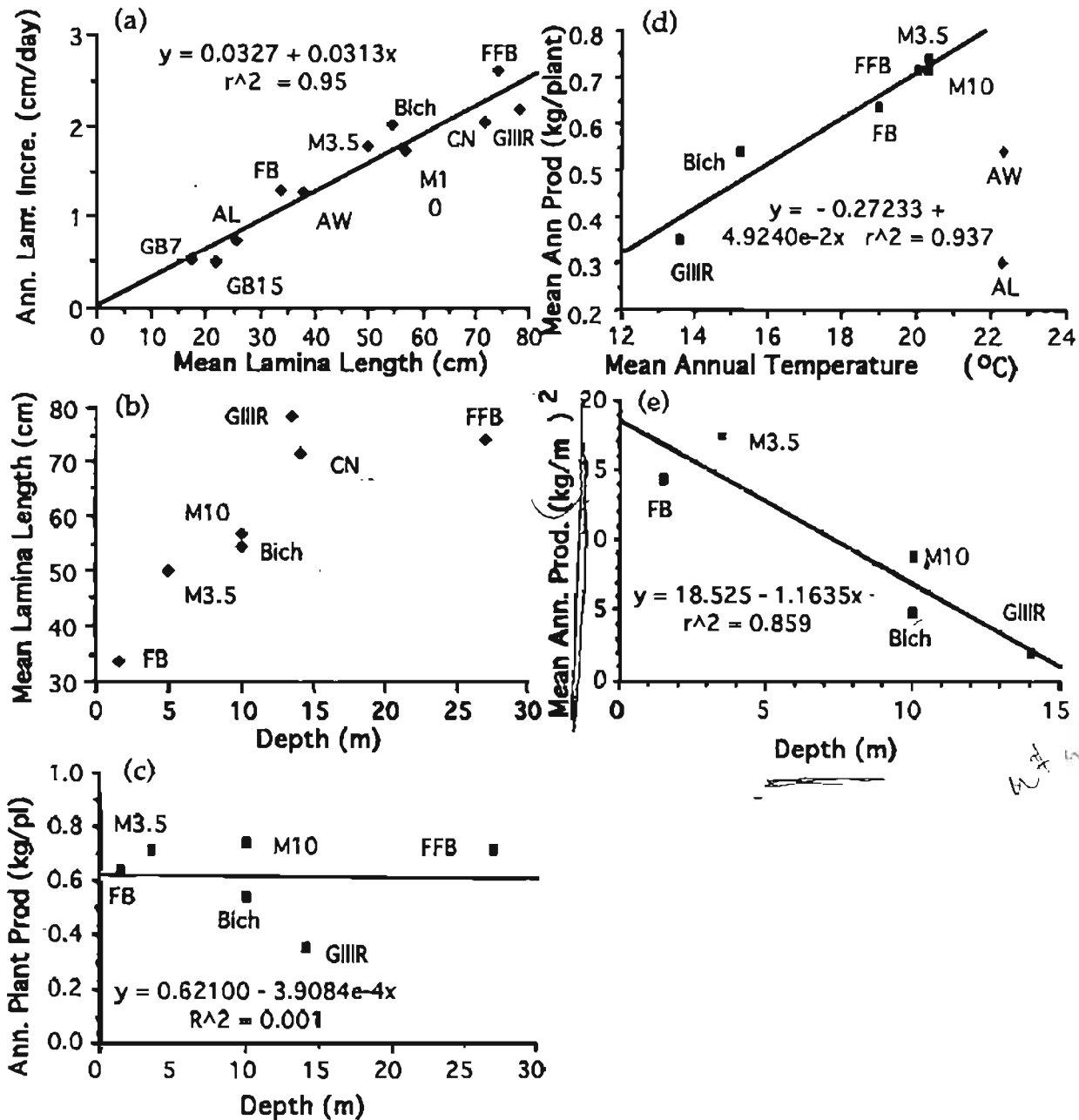


b) Bicheno



**Fig 3.10** Figures showing the relationship between a number of factors concerning *Ecklonia radiata* from published studies. Legend at bottom of page.

a) Graph of mean lamina increment versus mean lamina length b) Graph of mean lamina length versus depth, c) individual plant production versus depth, d) individual plant production versus mean annual temperature, and e) production per unit area versus depth.



LEGEND- GIIIR- George III Reef, Bich- Bicheno, Tasmania (this study), AW- Site W, Abrolhos Islands, AL- Site L, Abrolhos Islands (Hatcher *et al.* 1987), M3.5- Marmion Reef 2-5 m depth, M10- Marmion Reef 10 m depth, FFB- Five Fathom Bank, Western Australia (Kirkman 1981), CN- Cape Nothumberland, South Australia (Shepherd 1980), FB- Fairlight Bay, New South Wales (Larkum 1986), GB7 Goat Bay, New Zealand 7 m depth and GB15- Goat Bay, New Zealand 15 m depth (Novaczek 1984 b).

## PART 2, CHAPTER 4.

### MACROCYSTIS PYRIFERA

#### INTRODUCTION

*Macrocystis pyrifera* is distributed widely but mainly circum-antarctic between 40° and 60° S latitude. The plant is particularly plentiful around most subantarctic islands and the southern tip of South America. It extends up the South American coast almost to the equator, and up the southern half of New Zealand and all coasts of Tasmania except the north. In the northern hemisphere *Macrocystis pyrifera* is known only from the west coast of North America (Womersley 1987).

This plant has long been of economic interest, initially because of its high potash content and later as a source of alginic acid. There is a large operation, Merck Int., harvesting and processing *Macrocystis pyrifera* based in California. A company harvesting this alga was established in Tasmania in the early sixties but ceased operation in 1973 due to financial and technical difficulties exacerbated by low yields of *Macrocystis pyrifera* (Sanderson 1987). It is because of the commercial interest, the large size and the capacity for high growth rates that *Macrocystis* spp. have been the subject of much research.

Studies have been centred principally in California (eg. Jackson 1987, Neushul and Harger 1987, Zimmerman and Kremer 1986, Gerard 1982, Wheeler and North 1980 and North 1971) but others include those conducted in British Columbia (Wheeler and Srivastava 1984 and Druehl 1978, 1984), Southern Chile (Santileces and Ojeda 1984), Falkland Islands (Tussenbroek 1989 a, b and c), Kerguelen Islands (Asensi *et al.* 1981), New



Zealand (Kain 1982) and Tasmania (Cribb 1954b). Aspects covered include the genetics, growth, productivity, physiology, ecology and morphometrics.

A *Macrocystis pyrifera* plant may be 4-20 m high. It bears many fronds and attaches to the substrate at the base by a conical holdfast consisting of one or a few central erect stipes bearing branched haptera on all sides. The stipes branch subdichotomously 3-6 times shortly above the holdfast to give the fronds. The fronds are 4-20 m long and bear blades unilaterally in the upper portions. The fronds grow from an intercalary meristem in a broadly falcate terminal blade which progressively splits off new blades. A mature blade is 30-150 cm long and 5-15 cm broad and is attached to the stipe via an elongate-ovoid to sub-spherical vesicle, 4-12 cm long (Womersley 1987). The vesicles act as floats, keeping the fronds orientated vertically in the water column; the upper portions remain at or near the surface, where they often form a dense canopy. The plant produces spores formed in specialized blades called sporophylls, usually without vesicles near their bases. *Macrocystis pyrifera* has an heteromorphic alternation of generations, the spores giving rise to a filamentous stage (gametophyte) which then gives rise to gametes. Male and female gametes fuse giving rise to the zygote and thence the large sporophyte (Fig. 4.1).

Within Australian coastal waters *Macrocystis pyrifera* is confined to Tasmania. A second smaller species *M. angustifolia* occurs on the north coast of Tasmania and the south coast of mainland Australia. Intergrades of the two species are believed to occur down as far the D'Entrecasteaux Channel, south of Hobart. *M. angustifolia* may be distinguished by its smaller blades and stoloniferous holdfast and is usually found in waters 0-10 m deep, whereas *M. pyrifera* occupies deeper waters, 2 to 25+m.

In Tasmania, *M. pyrifera* has a preference for shores with a moderate exposure to wave action or subject to good water flow. The occurrence of the species is often determined by the availability of substrate given these

conditions. The plant seems susceptible to warmer nutrient-depleted waters so in recent years when the EAC has been evident and/or there is a following warm winter there has been a reduced amount on Tasmanian coastlines. In cooler years however, thousands of tonnes may be found on the central east coast and in the south-east. The west coast lacks sufficient protected (from wave action) areas to support significant quantities of this plant.

The decision to study this particular macroalga was taken mainly because the plant is relatively abundant at George III Reef and on the Tasmanian coastline. There is also much comparable research done on this species elsewhere. *Macrocystis* beds are also recognized as being very productive by the local sea urchin and abalone divers. The aim was to determine the seasonality and key environmental factors determining the growth strategy by correlating these results with monitored growth parameters. An indication of the productivity of the plant was also determined for comparison with other areas.

## METHODS

### Growth Measurement

At George III Reef, plants were selected in areas of moderate density close to the transect line. Initially this was in 10 m of water adjacent to the '200' mark of the transect line (see Fig. 2.4). These were healthy plants at the start of the program in mid-1986. By mid-1987, however, these plants were deteriorating and disappearing and it became apparent that healthier plants would be required for tagging, so the site was moved to the '140' mark in 12 m of water. At the end of 1987 these plants also disappeared and the next and following plants were used from the other side of the reef in 6-8 m of

water, adjacent to the '400' mark. Plants were sampled once a month for the first year and every two months thereafter (mean; 57 days).

At Bicheno, plants were selected in the vicinity of the other plant species monitored in 10 m of water. Again apparently healthy plants deteriorated and disappeared and alternative plants were selected in deeper water (14 m) in May, 1988. Unfortunately these also disappeared before any follow-up measurements were possible. As there were no other significant stands of *Macrocystis pyrifera* available in the vicinity at the time, there is only one year's data from Bicheno. Mean sampling interval was 56 days. Further follow up studies were done at Darlington on Maria Island as this was the site of one of the few remaining stands of *Macrocystis pyrifera* by mid-1989.

At each sampling session, fronds tagged during the previous session were harvested and fifteen new fronds were tagged with numbered sections of plastic surveyors tape. This was tied at a point behind the node closest to one metre from the apical scimitar (see Fig. 4.1). All fronds chosen were at least 2 m and less than 5 m long (always subtidal) and selected from different plants where possible. The number of internodes was counted from the tag to the ultimate slit (considered here as the apex of the stipe). This and the distance from the apex to the tagged node was measured to the nearest centimetre.

Fronds were not always easy to relocate especially in the denser canopies so recovery rates were not always an accurate indication of mortality or stipe loss.

Measurements of harvested fronds were taken at the earliest possible opportunity after harvest, usually the same day. Total length, distance to the tag from the base and distance from the tag to the apical slit was measured and the number of nodes counted for each distance. The frond was weighed and the number of sporophylls at the base of the frond noted.

In addition to regressing mean length and blade increment of the fronds against hydrological and physical parameters over the sampling period, the mean number of blades in the upper metre of the fronds, measured on the plants at the initiation of each sampling period was regressed against these same parameters for one, two, three and four weeks prior to the time of measurement. Gerard (1976) has noted that the number of blades in the final metre of the frond may be a good index of frond growth.

#### Morphometric details

At the completion of studies in late 1988, further morphometric data were required to substantiate comparable relative rates of growth from different sized fronds and for comparison with other studies. No significant stands of *Macrocystis pyrifera* now existed at either Bicheno or George III Reef. The best stand available was located south of the Darlington Jetty on Maria Island (see Fig. 2.1), at the northern end of the Mercury Passage. The plants there were in 3-8 m of water and the bed extended for approximately 200 m adjacent to the coast and 60 m wide at its widest point. While the area is sheltered from wave action, currents of moderate strength are often experienced in the Mercury Passage. As the site is adjacent to deep water off the southern end of Maria Is. and there are no significant freshwater discharges in the immediate vicinity, water clarity is good.

At a time judged to be a period of good growth, July 1989, fifty subtidal and surface fronds of different lengths were tagged in a similar manner similar to above. Depth at the base of the tagged fronds was noted. Fronds were harvested 19 days after tagging and measurements taken as above.

### Statistics

Statistics used in this chapter were the same as for *Ecklonia radiata* except for an equation which closely approximates the conventional means of describing the dependence of plant growth on nutrient concentration. This was used in a best fit non-linear regression program to estimate critical average nitrate concentrations.

This was;

$$\text{Growth increment} = a \times (1 - \exp(-b \times [\text{NO}_3])),$$

where  $[\text{NO}_3]$  is the mean nitrate (nitrate + nitrite) concentration between observations.

## RESULTS

### Morphometric data

Figures 4.2 a-c demonstrate a good linear relationship between the number of blades on a frond and length of the frond for each of the sites. Mean blade numbers of 94, 92 and 105 are indicated for fronds at the surface at each of the sites and 56, 53 and 53 for fronds three metres in length for Maria Is, George III Reef and Bicheno respectively (3 m is an arbitrary length, subtidal at all three sites). Internodal lengths for George III Reef and Bicheno fronds are similar but those at Maria Island are shorter.

Fronds of four different lengths from the Maria Is plants were chosen to demonstrate how internodal distances (Fig. 4.3) and weight distribution (Fig. 4.4) vary along the length of the fronds. There are initial large internodal distances in the older fronds corresponding to attachment of sporophylls, then a plateauing of internodal distances to a point less than a metre from the tip of the frond. The upper last metre corresponds to the distance over which there is still active elongation. Irregularities in

internodal distances occur for two metres around the part of the frond that coincides with the surface.

Biomass peaks occur at the region of mature blades roughly at the medial point of the frond. Biomass declines towards the base of the plant as the blades deteriorate and towards the apex with the less mature blades. Younger fronds have a smaller number of mature blades reflected in a lesser region of maximal biomass.

#### Growth increment

At Maria Is, to determine the effect of the depth on the change in length and the production of new blades, the measured depth of the base of the plant was subtracted from the total length of the frond to give the distance of the apex relative to the surface. This has been plotted against the increment in number of blades in Figure 4.5 a and increment in length for all fronds in Figure 4.5 b.

An increase in length increment by fronds as they approach the surface followed by a decrease afterwards is demonstrated for the plants at Maria Is. (Fig. 4.5 a). This agrees with the findings of Tussenbroek (1989a) for plants in the Falklands. Increment in the number of blades however, stays relatively constant for all depths after the frond achieves a minimum length of one metre. As the fronds approach their maximum length, at formation of the terminal blade, the rate of node production decreases, thus the decrease in blade increment for longer fronds in Figure 4.5 a.

Fronds have a set life-span and as this is approached, growth slows. Three of the fronds harvested had terminal blades where production had stopped. This was evidenced by the three lower measured growth rates.

Variation in the number of blades in the last metre of the frond for George III Reef and Bicheno plants with season is depicted in Figure 4.6. They show maximum internodal distances in early winter and minimum

in the summer at George III Reef. At Bicheno the maximum number of blades in the final metre of the frond occurs 2-3 months earlier than at George III Reef.

Blade production (Fig. 4.7 a) at George III Reef has a definite seasonality, with a peak in the springtime. Production of blades at Bicheno (Fig. 4.7 b) agrees largely with the pattern observed at George III Reef. Mean blade production at George III Reef was  $0.53 \pm .01$  blades per day, while at Bicheno it was 0.509 blades per day (0.507 blades per day at George III Reef for the same time period).

Length increment is apparently also seasonal at George III Reef (Fig. 4.8 a), with a major peak in winter and possibly a secondary, smaller rise in summer. The pattern at Bicheno (Fig. 4.8 b) agrees with these results. Mean length increment is  $5.3 \pm 0.4$  cm/day at George III Reef, with a maximum of 10.9 cm/day recorded for an individual plant over a single sampling session. Plants at Bicheno had an length increment of 5.0 cm/day with a maximum of 10.8 cm/day.

#### Regression against Physical and Hydrological Parameters.

Stepwise regression of daily sunshine, temperature and nutrients over three weeks prior to the measurement of the number of blades in the first metre of the frond indicate sunshine (SUNSHG) and temperature at 20 m (TEMP20) combined to have a high correlation, according to the following equation:

$$\text{No. Nodes} = 40.86 + 3.299 \times \text{SUNSHG} - 1.882 \times \text{TEMP20}, r = .736, p = .0093.$$

When the number of candidate predictors is taken into account (Wilkinson and Dallal 1981), the confidence interval of this best fit equation is reduced to  $p = .01$ .

Stepwise regression of environmental parameters against growth rate as expressed in terms of 1) blade increment or 2) length increment at George III Reef suggest for;

1) blade increment; temperature at 20m (TEMP20) in Storm Bay in conjunction with average nitrate concentrations over the period of measurement at 10m (NO310) with partial probabilities of  $p = .0001$  &  $.002$  respectively This is expressed as:

$$\text{Blade increment} = 2.101 - 0.106 \times \text{TEMP20} - 0.132 \times \text{NIT210}, r = 0.84, p = 0.0001.$$

However, when the number of candidate predictors is taken into account (Wilkinson and Dallal 1981), the confidence interval of this best fit equation is reduced to  $p = .01$ .

2) length increment was best described as a function of either adjusted swell or mean daily hours of sunshine, expressed as follows:

$$\text{Length Increment} = 7.568 - 0.46 \times \text{SUNSHG}, r = 0.437, p = 0.048$$

or

$$\text{Length Increment} = -0.898 + 3.916 \times \text{ADJSWELL}, r = .479, p = 0.028$$

When the number of candidate predictors is taken into account (Wilkinson and Dallal 1981), neither of these equations are significant.

#### FronD life expectancy

Individual fronds may be expected to have up to 150-180 blades at maximum size, according to Maria Island results. From the mean blade production rates, calculated life expectancy is at least nine months to one year for Tasmanian fronds. Occasional fronds may be longer lived. One



frond from the Maria Is population had 214 nodes with no evidence of a terminal blade.

### Sporophylls

Both Bicheno and George III Reef *Macrocystis* plants show a peak in the number of sporophylls per frond in late summer (Fig. 4.9). Presumably this timing ensures dispersion of the hardier gametophyte stage to overwinter. Juvenile sporophytes would then reappear in the spring time.

### Annual Productivity

An estimate of annual productivity may be obtained from the data. Mean maximal biomass of 5 node sections of three fronds (all with mature blades) from Maria Island (125, 152 and 192 gm, see Fig. 4.3 a) gives a value of 156 gm or 31 gm per blade and node. This figure contrasts with the values used by Kain (1982) of 50gm for New Zealand plants (measured growth rate of 0.5 blades per day over a 4-12 day period) and 33gm for faster growing Californian plants (measured growth rate of more than 1 blade per day over a 4-12 day period ).

Using this value and the mean blade increment of individual fronds at Bicheno and George III Reef annual productivity can be approximated (see table 4.2).

**TABLE 4.2.** Estimate of annual productivity of individual fronds of *Macrocystis pyrifera*.

	Mean increment blade/day	Estimated Average wet weight/blade (gm)	Annual productivity. (kg/frond/year)
George III Reef	0.532	31	6.0
Bicheno	0.509	31	5.8

Frond densities in *Macrocystis* beds can be very variable. A survey of the *Macrocystis pyrifera* along the east coast of Tasmania in 1986 (Sanderson 1987a) showed typical values in a moderately dense bed of 4 fronds per m<sup>2</sup>. Using the above production rates for fronds this gives a yearly productivity value of 24 kg/m<sup>2</sup> at George III Reef and Bicheno in year-round beds.

This value approximates total annual frond biomass production including that lost to erosion of blades, but excludes loss due to exudation of organic materials. Loss of biomass due to erosion, can be estimated as the difference between this value and the product of mean increase in length per year and mean weight per unit length. Mean weight per unit length is obtained from the total weight of harvested fronds, sampled throughout the year for Bicheno and George III Reef divided by their total length and are at George III Reef; 250 ± 20 g/m (n=43), Bicheno; 140 ± 10 g/m (n=57) and Maria Is; 169 ± 9 g/m (n=31).

**TABLE 4.3** Annual productivity estimations from mean length increase of fronds and loss to the system through erosion and degeneration of older tissues.

	Mean increment cm/day/frond	Mean wet weight/m (gm/m)	Net Annual biomass production (kg/frond/year)
George III Reef	5.25	250	4.8
Bicheno	5.0	140	2.6

Using the mean length increments, the following values are obtained for mean annual biomass increase for fronds at George III Reef and Bicheno (see table 4.3). Relative to the George III plants, a larger proportion of biomass production of the fronds at Bicheno would appear lost to erosion,

degeneration of older tissues and blade loss (provided the value used for maximum blade weight is reasonable).

Tussenbroek (1989) has shown for the Falkland populations of *Macrocystis pyrifera* that the production of blades in canopy fronds is similar to that of the submersed fronds yet biomass production may differ between the two by as much as a factor of five. The difference in production is due to the difference in the weight of the blades produced. Light is most likely the limiting factor affecting the production rate of the submersed fronds due to the shading affect of the canopy. Coverage of the canopy was never more than sparse to moderate at all three sites. Measurements at George III Reef within the kelp forest at 10m depth indicated a 25% reduction in light compared to outside the kelp forest.

## DISCUSSION

### Morphometric characteristics

Fronds of *Macrocystis pyrifera* from Bicheno and George III Reef have similar morphological characteristics to those examined elsewhere. Figure 4.4 b showing accumulating wet weight versus number of internodes from the apex is consistent with log-log relationships determined by Kain (1982) and Jackson *et al.* (1986). Table 4.4 compares parameters calculated from lines of best fit, for an arbitrary frond length of 10 m. Generally, plants in deeper water have longer internodal lengths than in shallow water. Sheltered fronds have shorter internode lengths and are usually heavier per unit length than those from more wave exposed sites. In this study, plants from George III Reef are heavier than east coast plants of a similar length.

**TABLE 4.4** Extrapolated number of nodes and weight of fronds 10m in length from selected studies, compared with this study.

Who	Where	Depth (m)	Exposure to wave action,	Nodes /10m	Wet wt/10m (kg)
North 1971	La Jolla, Calif.	10	moderate	107	1.7
Jackson <i>et al.</i> , 1985	La Jolla, Calif	20	moderate	61	0.713
Gerard 1976,	Monterey Bay, Calif.	10	moderate	81	1.47-2.33
Kain 1982	Aquarium Pt, New Zeal.	2-3	sheltered	101	?
Santileces & Ojeda 1984	Puerto Toro S. Chile.	0.5-10	sheltered-moderate	63	?
Tussenbroek, 1989.	Stanley Hbr, Falklands	0-4	sheltered	120	1.67
	Kelly Rocks Falklands	5	Moderate	69	1.19
Sanderson, 1985-1989.	George III Reef, Tas.	6-12	Moderate	98	2.98
	Bicheno Tas.	10	Moderate	101	1.21
	Maria Is Tas.	4-6	sheltered	145	1.83

#### Growth parameters

In this study the number of blades in the first metre of the frond was found to vary seasonally with good correlations to length and blade increment of the fronds ( $-0.566$ ,  $p < .05$  and  $0.537$ ,  $p < .05$ , respectively). This agrees with findings of Cribb (1954) and Pace (1972) who noted an increase in the number of blades attached to the apical blade with an increasing rate of new blade formation. Gerard (1976) also had similar good correlations with blade increment and noted that this attribute could be a useful index of frond growth. Given the possible relationship between

length and water movement however water movement may have a influencing affect.

Seasonal variation of blade increment and length increment at George III Reef appears to show different periodicities. Blade production is maximum in the spring-early summer whereas length increment is maximum in winter with possibly a minor peak in the summer. Despite the long period for which *Macrocystis* has been studied in California, only recently has any seasonality been detected (Zimmerman and Kremer 1986), and this has been offshore of the coast on Santa Catalina Island. Here frond extension was maximum in the winter and least in late summer. In contrast, frond initiation (as distinct from blade initiation) rate is maximum in summer. If frond initiation rate is comparable to blade initiation, then the seasonality matches the results here. In the Falklands however, blade initiation closely matches length increment of the fronds at exposed, nutrient-abundant and sheltered, nutrient-limited sites for the entire year with maximums for both factors in the spring to late summer period (Tussenbroek 1989 a). It is difficult to envisage why there is this difference considering many other similarities.

Regression of length increment against swell indicated a possible positive relationship. There is also an increase in length increment as fronds approach the surface and generally, exposed sites have longer nodes than sheltered sites. Swell and water movement thus appears to influence stipe elongation. Morphological plasticity in response to water motion has been noted previously for other species in the Laminariales (Gerard and Mann 1979, Norton *et al.* 1982). Perhaps water movement is greatest in the summer in the Falklands resulting in greater extensions of the internodes over this period.

### Nutrient availability

Stepwise regression of growth rate as indicated by increment in the number of blades produced per day reveals temperature and nitrate concentration as being very significant factors affecting rate of production. Zimmerman and Kremer (1986) have evidence to support storage capacity of nitrates in *Macrocystis* of approximately one month in California and nitrogen reserves lasted two weeks in plants transplanted by Gerard (1982a) to a low nitrogen environment. Regression of average nitrate concentrations for 2 weeks and 4 weeks (CSIRO data) extra to the measurement interval gave slightly better regressions against blade increment and length increment for plants at George III Reef (all  $p < .05$ ).

Zimmerman and Kremer (1986), fitted negative exponential growth curves to growth rates versus average nitrate concentrations and also, but less successfully for temperature (following from the linear relationship between nitrate concentration and temperature in California). A significant fit for nitrate concentrations for both length increment and blade increment is found for this data using a negative exponential growth curve (see Fig. 4.10 both  $p < .05$ ). Length increment is possibly not as reliable due to the effects of extrinsic factors of water motion and light. Nitrate saturation is achieved at average concentrations of between 0.3 and 0.9  $\mu\text{M}$   $[\text{NO}_3]$  for length increment and 0.4 and 1.0 for blade increment. This compares with 1.5-2.0 and 1.5-3.0  $\mu\text{M}$   $[\text{NO}_3]$  respectively for frond elongation and initiation over one month found by Zimmerman and Kremer (1986) at Catalina Is.

Temperature may be expected to display the mirror image of this relationship due to the inverse linear relationship, demonstrated in chapter 2, that exists between temperature and nitrogen in shallower waters. In fact Deysher and Dean (1986) and Zimmerman and Kremer (1986) have suggested the use of temperature as an indicator for nutrient levels once the

relationship between the two is known. This enables high frequency sampling of nutrient status and thus a more comprehensive picture of the environment affecting the plants. In this study, temperature appears to have an inverse negative exponential relationship to length increment, but with blade increment it is not as obvious, with the relationship closely approaching a negative linear relationship (see Fig. 4.10).

### FronD Age

FronD ages of 9-12 months at Bicheno and George III Reef compares with estimated ages of 6 months by North (1961, 1971) and by Gerard (1976) of 5.5 to 6.5 months for fronds formed in the summer and 7 to 7.5 months for fronds formed in the winter and autumn for Californian plants. Cribb (1954b) recorded a maximum age between 7 and 10 months for plants at Port Arthur, but does not explain fully how the result was obtained. The calculated ages in this study compare well with those found by Tussenbroek (1989b) for the Falkland Island plants of 12 months with occasional fronds having an estimated age of 12-13 months.

Tussenbroek accounts for the difference in age between the Californian plants and those from the Falklands by the higher productivity of the Californian plants, as the maximum number of nodes of fronds from both places was similar, at 160. The productivity difference between the Tasmanian and Californian plants may be explained similarly.

### Comparative production of *Macrocystis pyrifera*

Rate of blade increase would seem to give a more direct indication of the production of *Macrocystis pyrifera* than length increment as it does not appear to be as subject to extrinsic factors. Length increment or extension of the stipe reflects growth of the plant but may be affected by water motion or light (see regressions above). Even taking these factors into

account, productivity of Tasmanian plants is on a par with the New Zealand and the open-ocean Falklands Islands plants (see table 4.5, page 134). Plants in California are the most productive, with plants adjacent to the coast more productive than plants from Santa Catalina Is, approximately 50 kilometres off-shore. Plants from the Kerguelen Islands are the least productive.

Tussenbroek (1989a) attributes the difference between the Kerguelen and Falkland Islands plants to temperature differences of the water, as both places are at similar latitudes and there are no apparent nutrient problems at either place. The open-ocean Falkland Islands plants however, while having similar annual production to the Tasmanian plants, are further south (less light) and in cooler waters. The similarity in production, despite these apparent negative influences is possibly due to the higher nutrient levels in the water surrounding the Falklands. Plants at Kelly rocks, on the Falkland Islands were not exposed to nutrient limitation at any time during the year.

The Tasmanian and the New Zealand plants are situated similarly with respect to the subantarctic convergence and show similar productivities. The greater productivity of the Californian plants can be explained by the lower latitude of the sites and thus greater light availability and to the occurrence of periodic upwelling off the coast. The plants at Santa Catalina Island would appear not to be as subject to these nutrient enriched waters and appear slightly less productive.

### Comments

Charles Darwin wrote after observing the kelp forests of Tierra del Fuego (Darwin, 1860 p. 227-229 and Gerard, 1976).

"There is one marine production, which from its importance is worthy of a particular history. It is the kelp, or *Macrocystis pyrifera*



..... The number of living creatures of all Orders, whose existence intimately depends on the kelp, is wonderful ..... I can only compare these great aquatic forests of the southern hemisphere, with the terrestrial in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp."

The presence of these kelp forests on the coast enhances the productivity of an area and increases niche availability. Tasmanian urchin divers and abalone divers believe the beds of *Macrocystis* are better areas for production of their respective livelihoods. Fish species diversity is also enhanced in the vicinity of *Macrocystis* forests. For these reasons *Macrocystis* forests can be and are an important part of the marine ecosystem on Tasmania's coast.

Cribb's (1954b) estimated the harvestable quantities of *Macrocystis* on the east coast of Tasmania to be in the vicinity of 355,000 tons of wet weed per year assuming three harvests a year, or 120,000 tons with one harvest. In the late sixties, a company was started on the east coast of Tasmania to harvest and process *Macrocystis*. By the early seventies however, due to financial and technical difficulties exacerbated by low yields of *Macrocystis pyrifera*, the company closed. A survey done in 1986 showed there to be only to be only 12,000 tonnes of the alga available per year (Sanderson 1987a) and since then the amount of the alga has dropped (by 1989) to levels estimated to be about one tenth the estimates in 1986.

Many theories have been postulated as to the cause of the demise of the alga over the years, by a range of people associated with coastal waters including fisherman, aquaculturists, divers and scientists. Theories include the activities of the harvesting company, an increase in sediment in the water due to clearing of terrestrial forests and consequent increased run-

off, activities of professional and amateur fishermen close to the shore in motorized boats which chop up the surface frond of the alga and the overfishing of the crayfish populations which kept the herbivores of the *Macrocystis* (such as the sea-urchin *Heliocidaris erythrogramma*) under control. Cribb's technique in assessing the populations due to limited and now antique resources may also be questioned.

Harris *et al.* (1988), used CSIRO records of water temperatures off the coast of Maria Is. since 1946 to observe that there has been an increase in the maximum summer temperature of one degree Celsius to the present. This has been concurrent with decreasing effects of El Niño Southern Oscillation (resulting in cooler waters in Tasmania) and an increasing incidence of the incursion of the warm, nutrient depleted, East Australian Current down the eastern side of Tasmania. These effects have also occurred in conjunction with the decline in *Macrocystis* populations off the Tasmanian coast. Also, in the 5-6 years prior to Cribb's (1954) estimate, temperatures were low for a few consecutive years. This in conjunction with increased boating activities of recreational and professional fisherman in near shore coastal waters may have contribute to the different estimates in the amount of *Macrocystis*.

A recent report by North (1989) claims that the condition and quantities of *Macrocystis* off the coast of California has never been better despite concern as to the lack of *Macrocystis* in previous years. According to North, despite the controversy about effects of human activities such as kelp harvesting and marine waste disposal on kelp beds of the Southern Californian Bight, the recent favourable conditions (La Niña, the period prior to an El Niño) clearly illustrates the overriding influence of oceanographic climate on *Macrocystis* populations in this region.

The results of this study have shown the *Macrocystis* in Tasmania behaves similarly to the Californian populations. Low nitrate

concentrations appear to result in nutrient limitation and lowered growth rates. The decline in *Macrocystis* is possibly due to the warming of the coastal waters and consequent reduction in available nitrates since 1954. If so, we may see the loss of *Macrocystis* from Tasmanian waters in the near future given the continuing warming trend of the coastal waters, and thus the loss of a potentially very important contributor to the local ecosystem.

Given the fact that *Macrocystis* is in a more marginal habitat in Tasmania than in California and the potentially large contribution of this alga to the local ecosystem, then perhaps activities that may have a deleterious affect on its existence such as result from the activities of fisherman etc. should be examined more closely.

The warming of coastal waters experienced here is possibly due to an approximately 22 year cycle of warming and cooling (Harris pers. com.). However it does provide a timely illustration of what we might expect from the longer term effects of Green House warming on sensitive algae such as *M. pyrifera*.

## SUMMARY

Mean length increment is  $5.25 \pm 0.35$  cm/day at George III Reef, with a maximum of 10.9 cm/day recorded for an individual plant over a single sampling session of 17 days. Bicheno plants had a length increment of 5.0 cm/day with a maximum of 10.8 cm/day over 75 days.

Mean blade production George III Reef was  $0.53 \pm .01$  blades per day with a maximum of 1.03 blades per day over 65 days, while at Bicheno it was 0.509 blades per day (0.507 blades per day for the same time period at George III Reef) and a maximum of 1.71 blades per day over 45 days.

Seasonality of length increase is the opposite in Tasmania to the Falklands (Tussenbroek 1989a), despite a similar seasonality to blade

increase - reason unknown. It is postulated that length increase may be influenced by water motion and this may be affecting differences in the seasonality.

Productivity is best determined from rate of blade production because change in length may be affected extrinsically by factors of swell and light.

A fit of negative exponential relationship to growth versus nitrate concentration indicates nitrate saturation at average nitrate concentrations 0.3 and 1.0  $\mu\text{M}$   $[\text{NO}_3]$  over a period of two months.

Annual productivity of *M. pyrifera* at the two sites suggests similar frond productivities of 6 kg/frond/yr. For a typical density of 4 fronds per  $\text{m}^2$  this results in estimates of 24 kg/ $\text{m}^2$  wet weight.

A greater percentage of plant material is lost from the fronds at Bicheno than at George III Reef caused by erosion other than loss of entire fronds and organic secretions.

Growth studies indicate *M. pyrifera* in Tasmania is more productive than *M. pyrifera* in the Kerguelen Islands, as productive as *M. pyrifera* in New Zealand and the Falkland Islands but less productive than *M. pyrifera* in California. These differences are believed to be attributable to more daylight and higher nutrient availability in California because of upwelling, and the colder waters in the Kerguelen Islands. The Falklands are in cooler waters but nutrients are more available. The New Zealand plants studied occupy a similar position latitudinally with respect to the sub-antarctic convergence and a similar productivity.

Tasmanian populations of *M. pyrifera* appear to be declining. This is occurring in conjunction with an overall warming of coastal waters. It is possible that *Macrocystis pyrifera* in Tasmania may be an early victim of the Greenhouse effect if it exists.

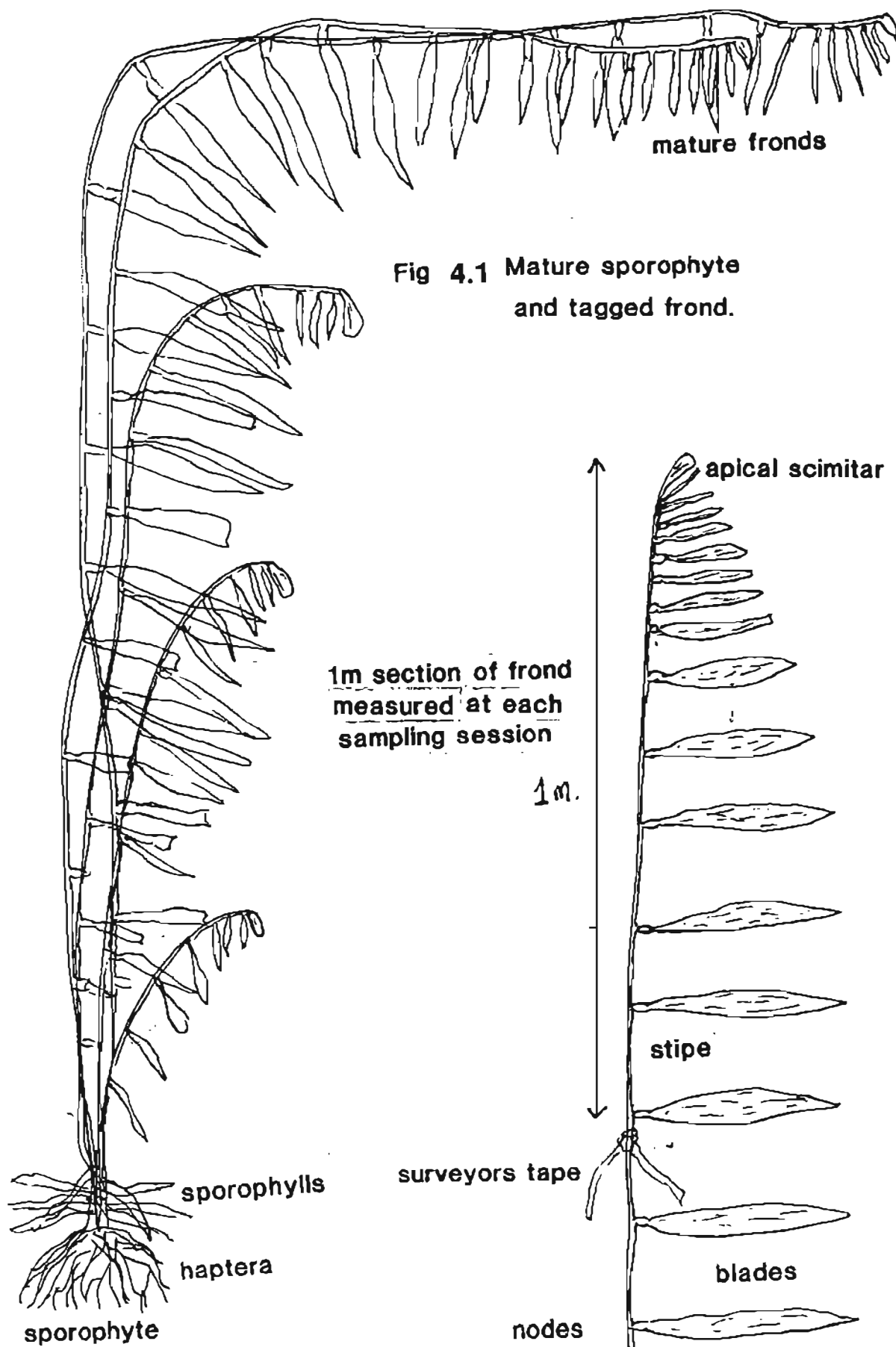
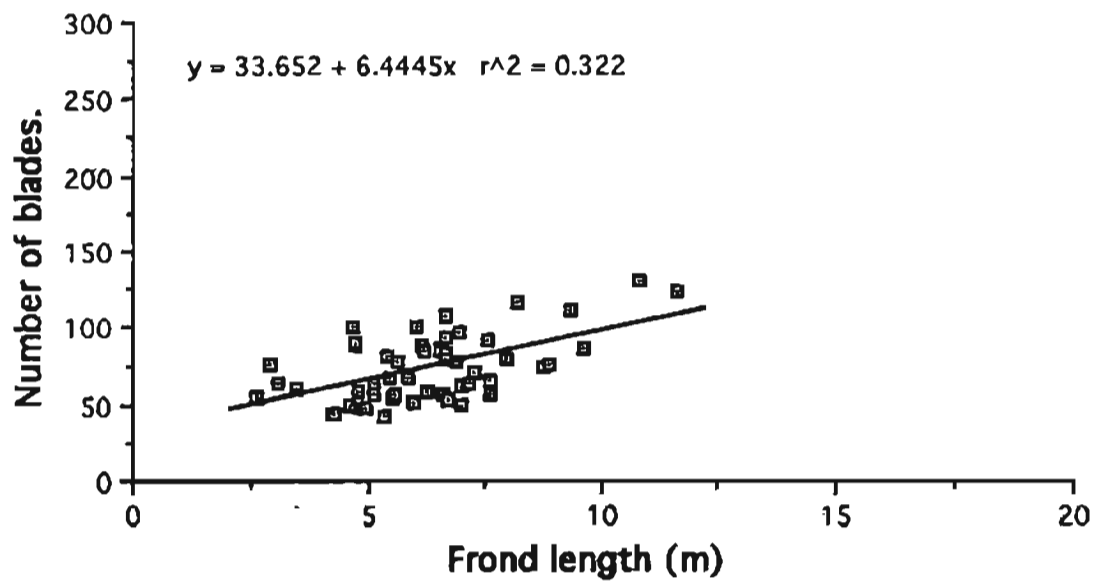


Fig. 4.2 Total number of blades versus total length for *Macrocystis* fronds.

a) George III Reef



b) Bicheno

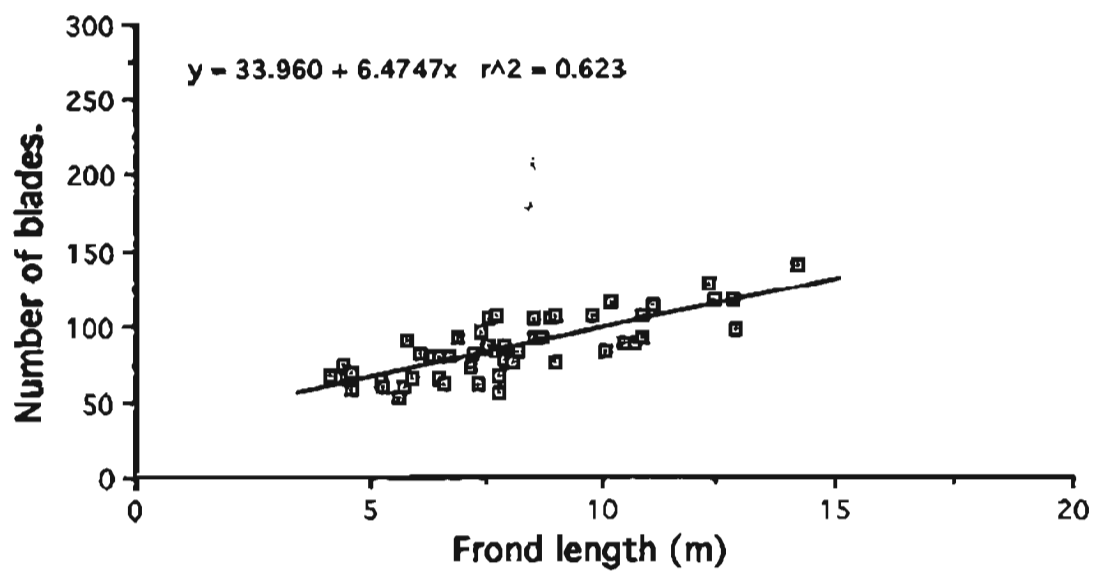
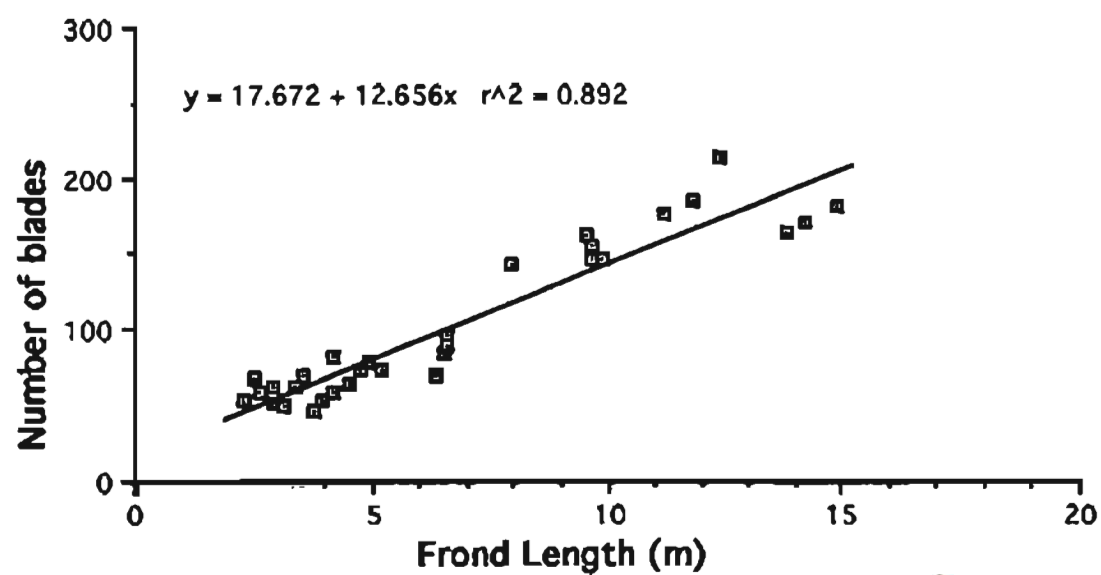
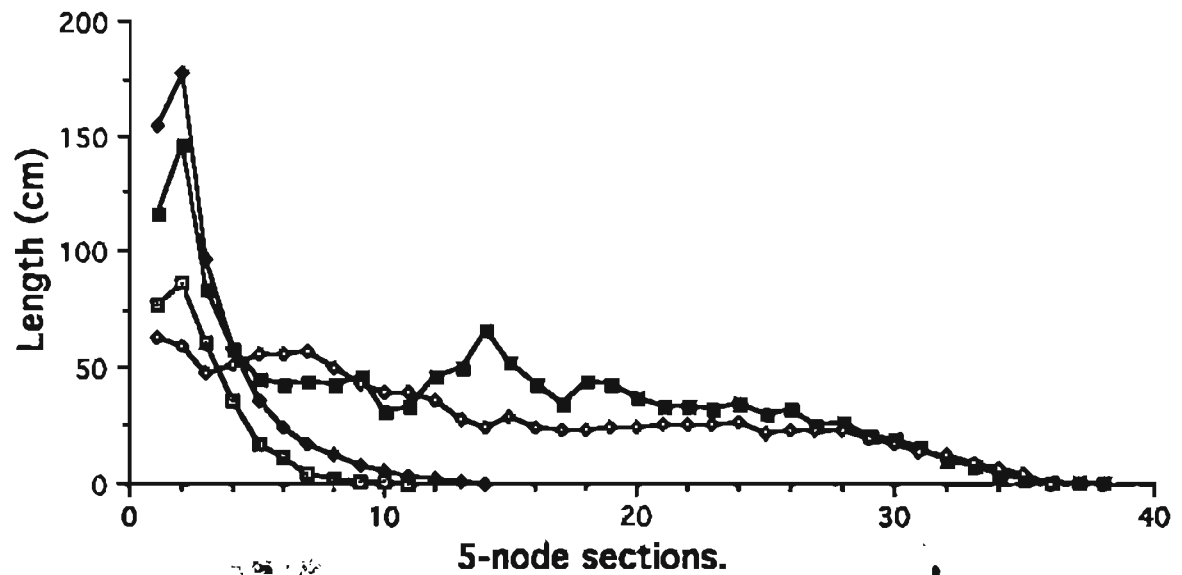


Fig. 4.2 Total number of blades versus total length for *Macrocystis* fronds.

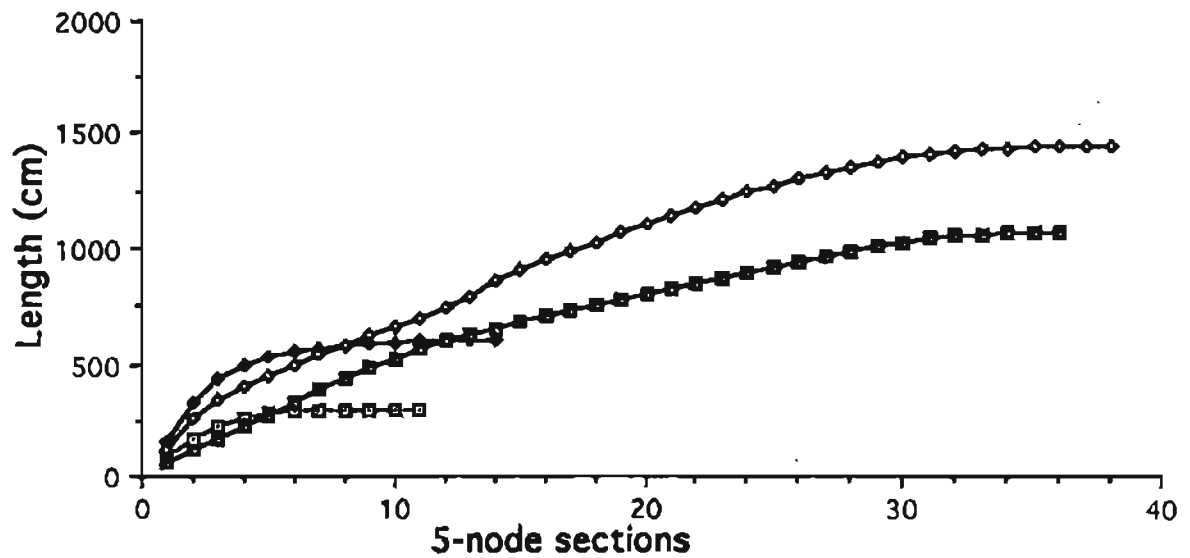
c) Darlington, Maria Island.



**Fig. 4.3 a)** Length of 5-node sections from the base to the tip of four different length fronds harvested at Maria Island on 14/7/89.

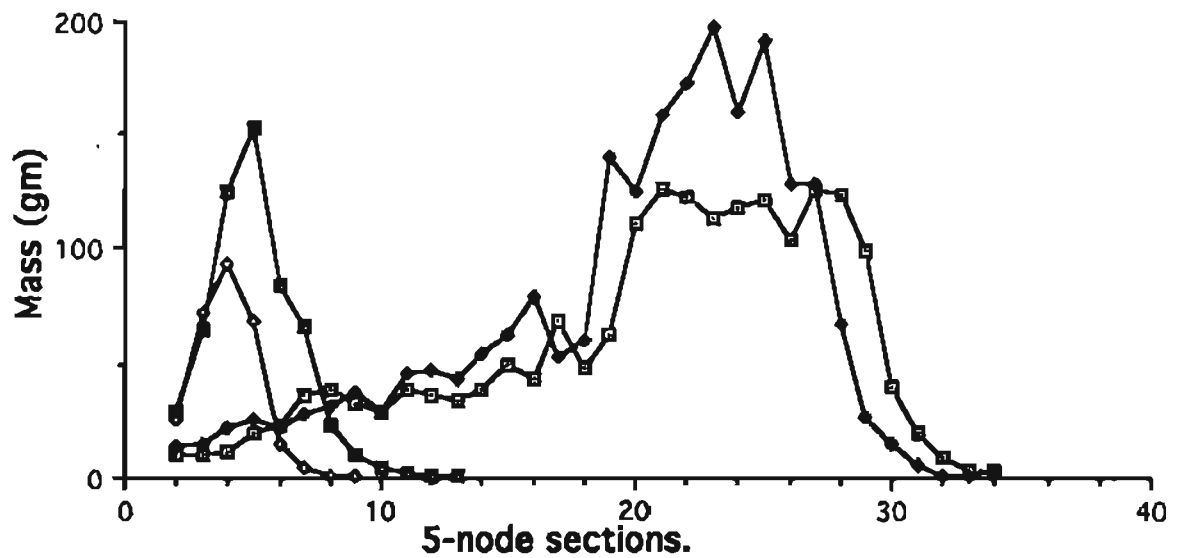


**Fig. 4.2 b)** Cumulative length of four different length fronds.

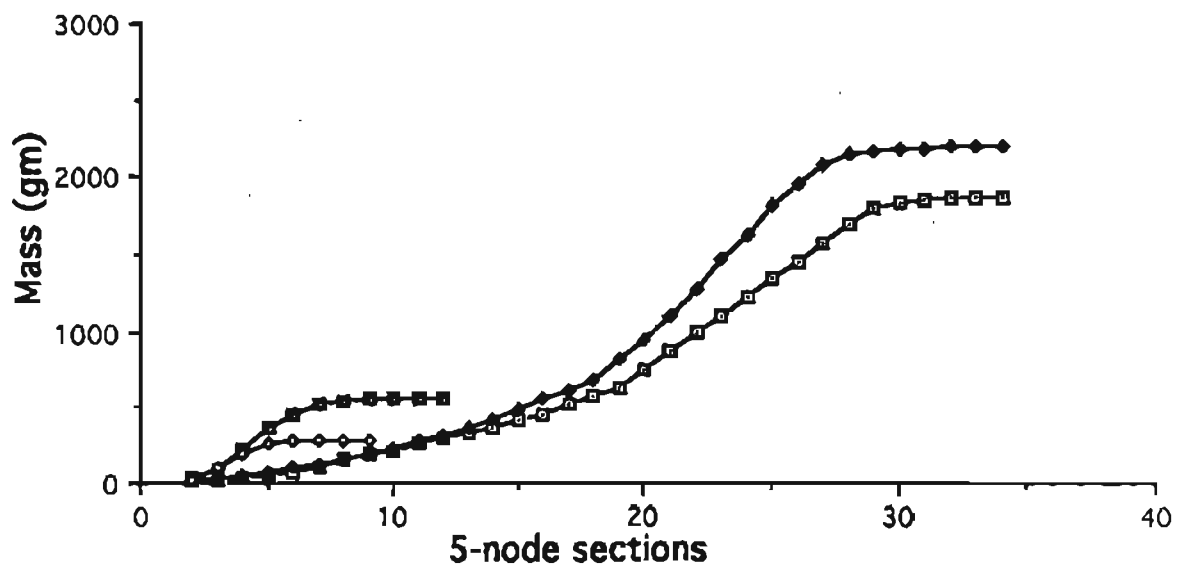




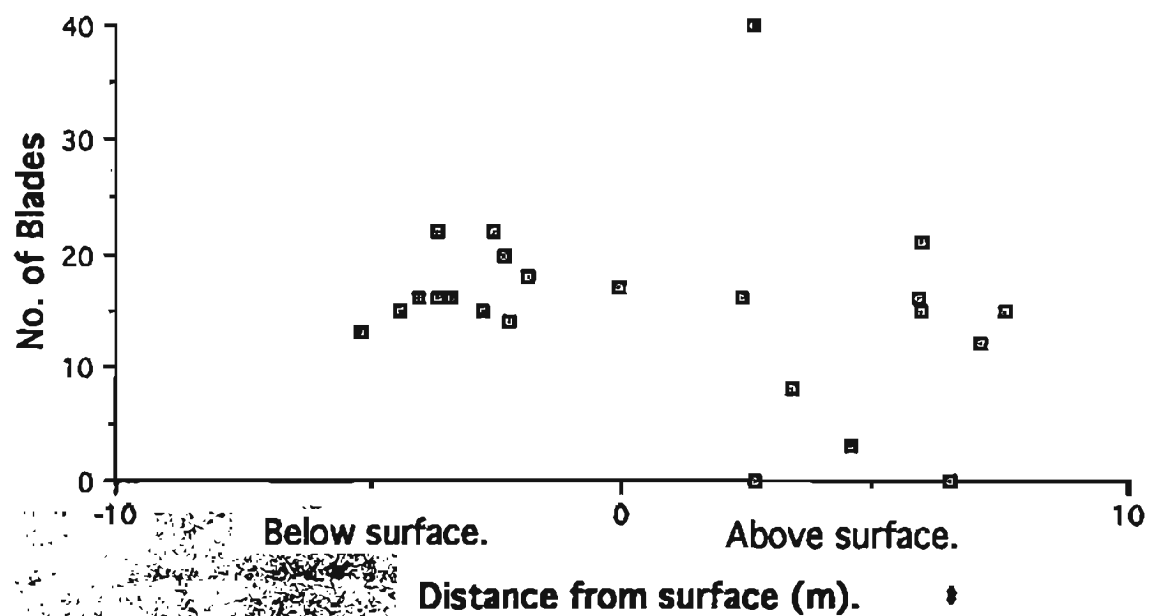
**Fig. 4.4 a)** Weight of 5-node sections from the base to the tip of four different length fronds harvested at Maria Island on 14/7/89.



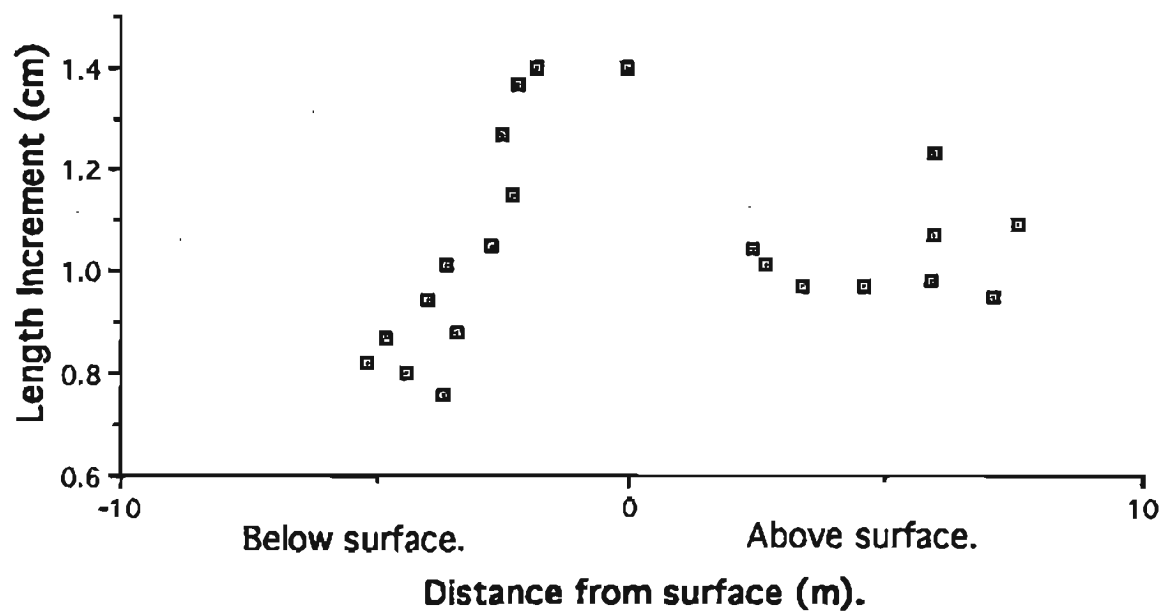
**Fig. 4.4 b)** Accumulative weight of four different length fronds.



**Fig. 4.5 a)** Increment in number of blades against distance of apex from surface of water of fronds harvested at Maria Island on 14/7/89.

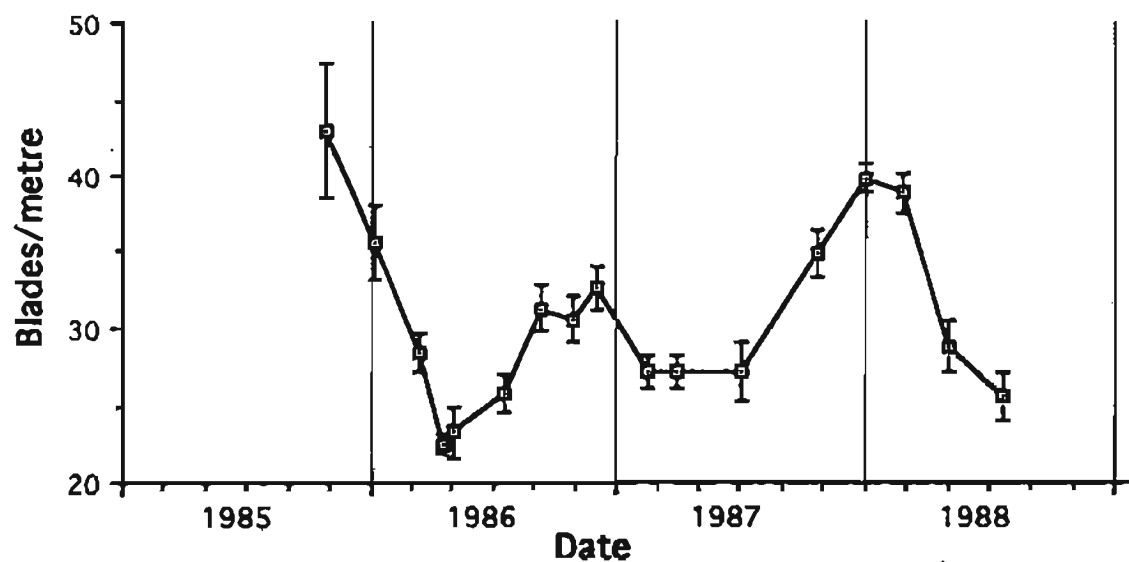


**Fig. 4.5 b)** Increment in length against distance of apex from the surface of the water. Bottom depth varied from 4-6.4 m.

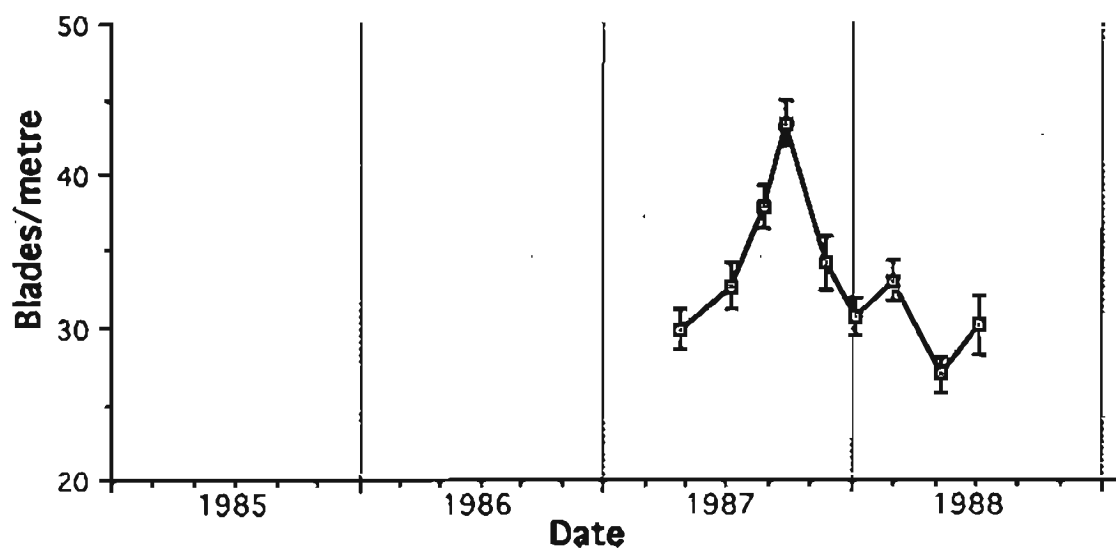


**Fig. 4.6** Seasonal variation in the number of nodes in first meter from apex on tagged fronds.

**a) George III Reef**

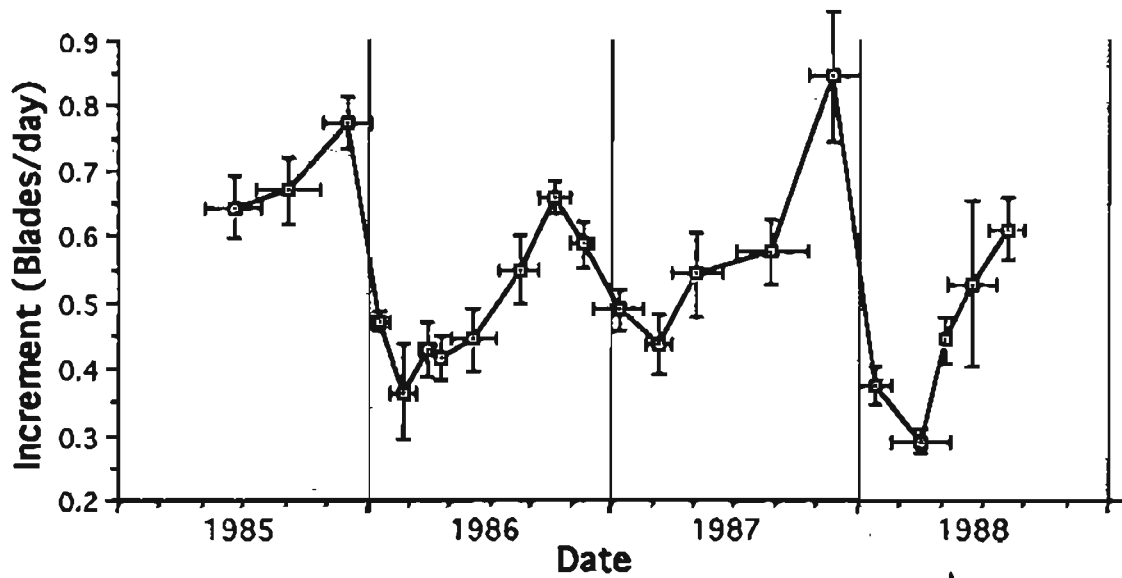


**b) Bicheno**



**Fig. 4.7** Rate of blade production on tagged fronds. Horizontal bars are sample period and vertical bars are standard error.

**a) George III Reef**



**b) Bicheno**

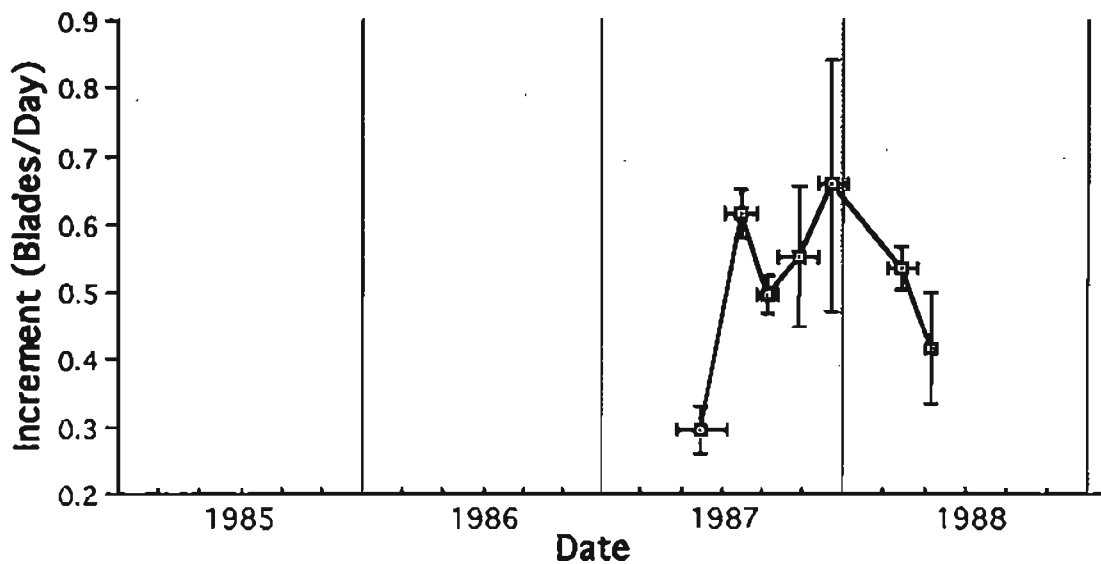
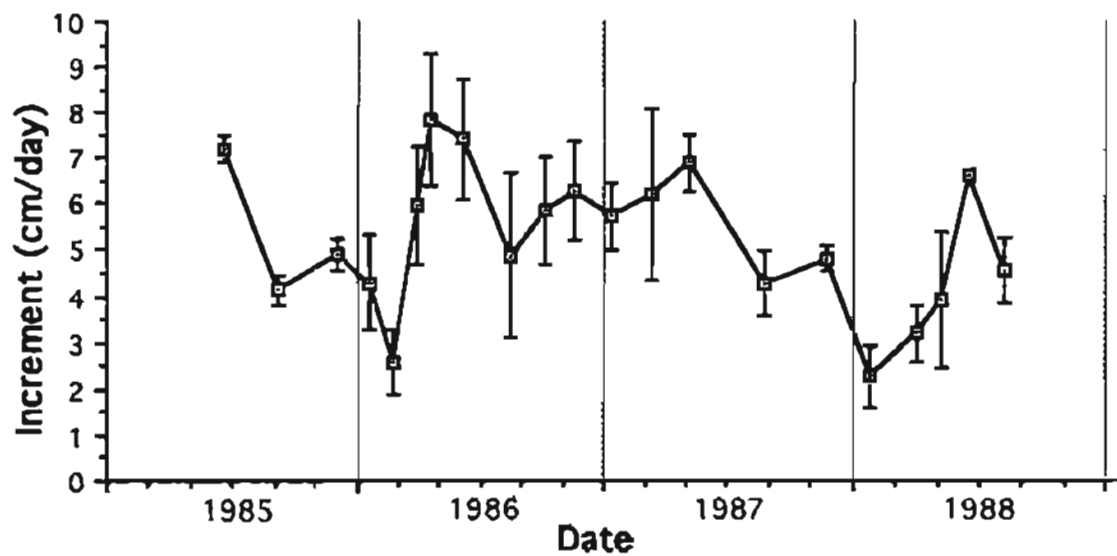


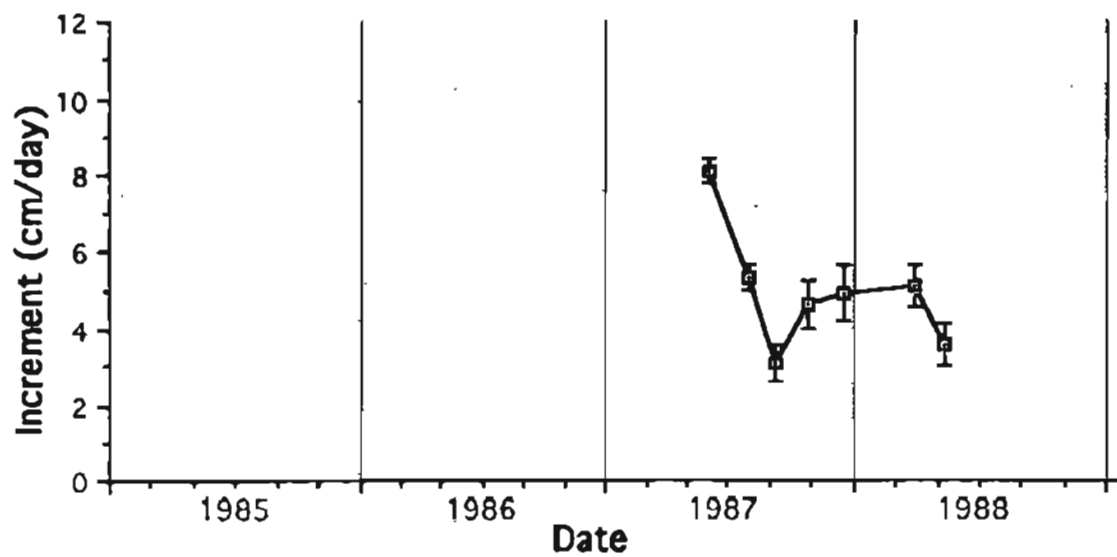


Fig. 4.8 Rate of increase in length of tagged fronds.

a) George III Reef.



b) Bicheno



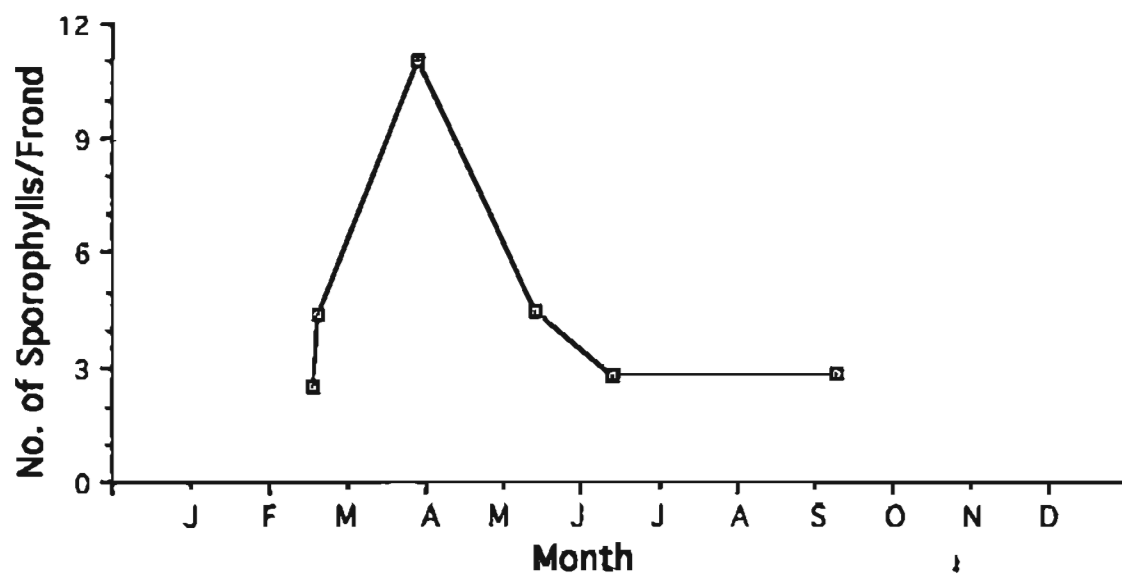
**Table 4.5** Mean growth per day monitored on canopy and submersed *Macrocystis pyrifera* fronds from various studies, worldwide.

Study	Location	Submersed/ Canopy	cm/day	Blades/ day	
	g/day				
North 1971	La Jolla, Calif.	Both	7.0-25	1.3*	
Gerard 1976	Monterey Bay, Calif.	Canopy	18-25 47 (max.)	1.1-2.0	
Zimmerman and Kremer 1986.	Santa Catalina Island, Calif.	Submersed	5.0-15.0		
Tussenbroek 1989a	Falkland Islands				
	Stanley Hbr	Submersed	0.5-3.0	0.12-0.34	0.5-3.0
	(protected)	Canopy	1.3-4.0	0.14-0.44	-2.0-20
	Kelly Rocks	Submersed	1.8-3.5	0.15-0.35	0.8-5.8
	(open-ocean)	Canopy	4.0-7.0	0.25-0.48	5.0-32
Asensi <i>et al</i> 1981	Kerguelen Is.		1.0-2.0	0.2-0.3	
Kain 1982	Aquarium Pt., 25*	Canopy	←	0.5*	
	New Zealand Pt Loma, Calif.	Canopy			36*
This study, Tasmania	Bicheno	Submersed	2.0-9.0	0.3-0.65	23.1
	George III Reef	Submersed	2.0-10.0	0.3-0.85	19.4
	Maria Is.	Submersed	5.7*	0.9*	
		Canopy	3.6*		
Cribb 1954	Port Arthur, Tasmania.	Canopy	3.4*	0.5*	
Lobban 1978	British Columbia	??	4	0.4	
<i>Macrocystis integrifolia</i>					

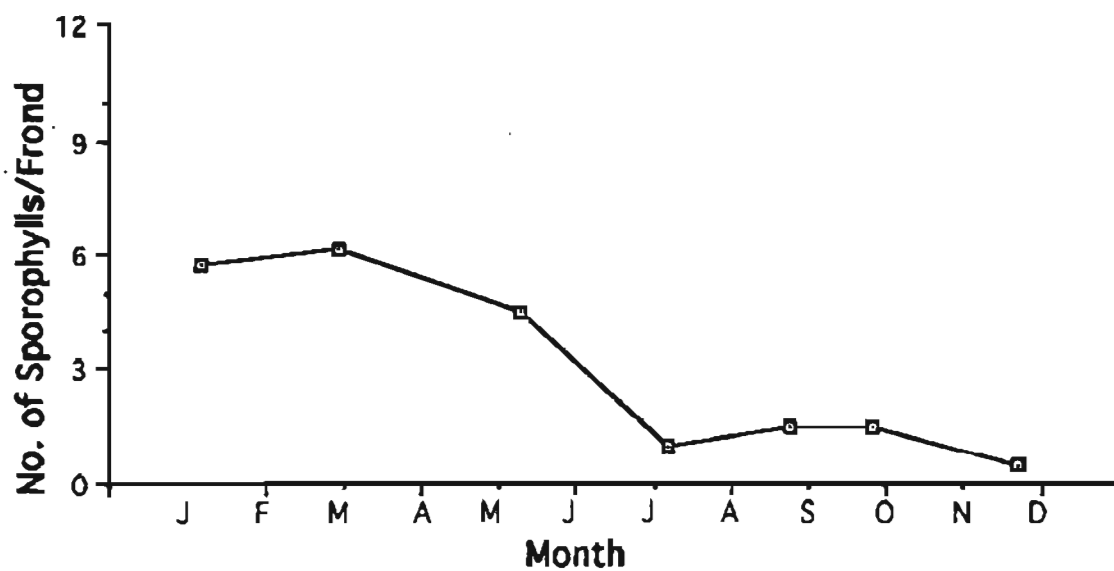
\* :- study only conducted for part of the year.

Fig. 4.9 Mean number of sporophylls on harvested fronds.

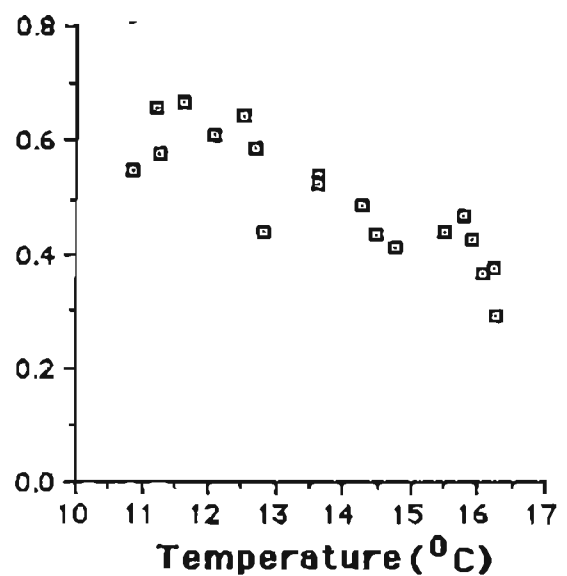
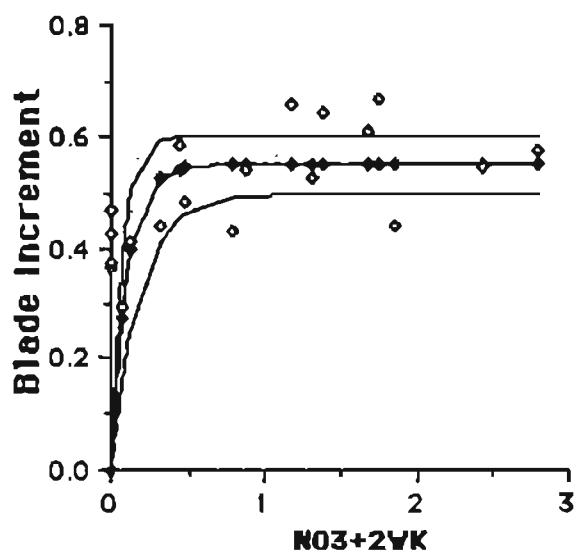
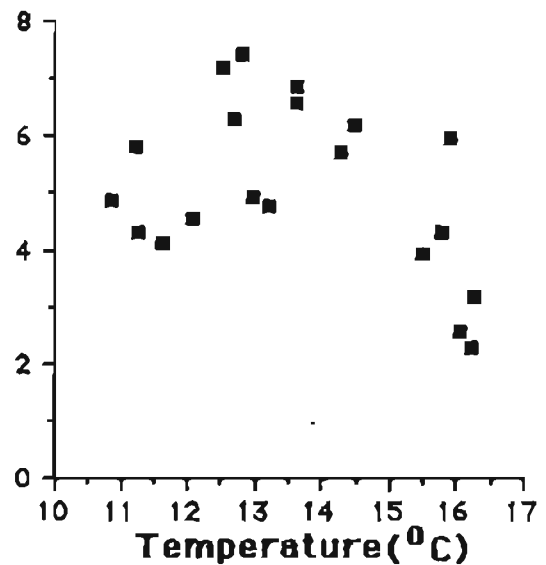
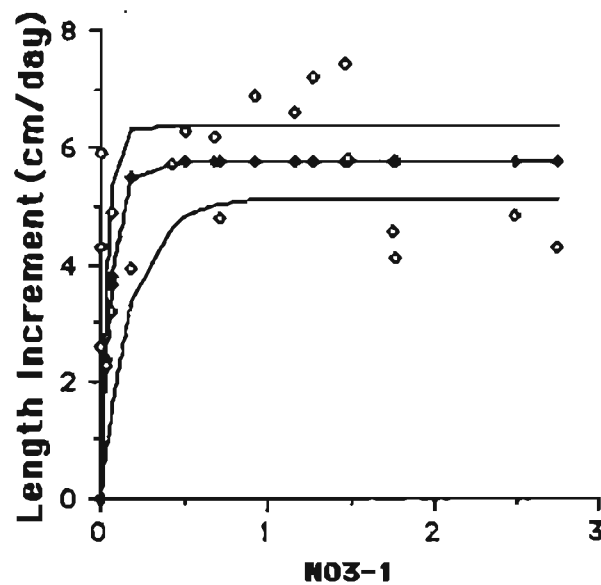
a) George III Reef.



b) Bicheno



**Fig. 4.10** Length increment and blade increment plotted against mean temperature and mean nitrate concentration (+1 month for length, +2 wk for blade) for George III Reef data. Negative exponential model has been fitted for nitrate data (with standard error ).





## PART 2, CHAPTER 5.

### TRANSPLANT AND DEVELOPMENT OF JUVENILES OF ECKLONIA RADIATA AND MACROCYSTIS PYRIFERA.

#### INTRODUCTION

The aim of this section of the study was to reveal whether any ecotypes had developed amongst the species investigated during adaptation to the different environmental regimes at Bicheno and George III Reef. This would be done by transplanting juveniles between the sites and monitoring changes. The transplants would be compared with local plants at the same life stage, having undergone similar treatments associated with transplantation. The initial intention was to incorporate plant tissue analysis for determination of possible nutrient stress. This was dropped due to technical difficulties. The following is the results of observed and measured differential growth and morphometrics of transplants and controls.

Ecotypes are manifestations of variation below the species level that are genetically fixed and adaptive to the environment (Davis and Heywood 1963). Ecotypes for macroalgae have been demonstrated for morphological traits (Chapman 1974), nitrogen assimilation characteristics (Espinoza and Chapman 1983), light-related traits (Gerard 1988), salinity (Yarish *et al.* 1979) and heavy metal concentration (Wilkinson 1974).

In this part of the study, three species of algae were originally investigated; *Phyllospora comosa*, *Macrocystis pyrifera* and *Ecklonia radiata*. Studies on *Phyllospora comosa* were not continued as the plant comes from a high surge area and the development of a means of securing the plants in

this area at George III Reef proved beyond the scope of this project. The *Macrocystis* juveniles proved difficult to maintain, due to adverse conditions affecting all *Macrocystis* stocks over the period of the study and the problems associated with transplanting these rapidly developing large plants. At George III Reef they either died back soon after transplantation or disappeared and the longest-lived was no more than 2-3 months. At Bicheno they survived for six months before their demise. This coincided with warmer waters and swells and occurred in conjunction with the loss of the local *Macrocystis* population in the vicinity of the study site. *Ecklonia radiata* transplants were more successful however.

For ease of description, plants transplanted from Bicheno to George III Reef will be referred to as 'B-G', from George III Reef to George III Reef as 'G-G', from George III Reef to Bicheno as 'G-B' and Bicheno to Bicheno as 'B-B'.

## METHOD

### Transplanting

#### *Ecklonia radiata*

Transplantation of plants took place before spring as it was decided that this would give them the greatest chance of survival. Juveniles of 10-20 cm in length were selected from the immediate vicinity of the areas of study at the respective sites. All transplants within and between sites were maintained in aerated sea-water at 15°C after harvest, and re-planted within days. Conditions for transplants and controls were kept as similar as possible.

Plants were secured at each site by elastic bands around bricks (see Fig 5.1). Where it was likely that plants may be subject to movement by surge bricks were tied to each other and to boulders.

Thirty B-G plants were transplanted initially in April 1987. As the survival rate was high, only fifteen were transplanted from George III Reef to Bicheno (G-B) and fifteen local plants (B-B & G-G) established as controls at both of the sites. Transplants at Bicheno were initiated in July 1987.

At George III Reef, plants were established close to the *Ecklonia* plants used in the main study in 14 m of water adjacent to the '0' mark. At Bicheno, plants were established close to the area of the other plants monitored.

On a regular basis, approximately every eight to ten weeks (mean; 62 days at George III Reef and 50 days at Bicheno), the plants were measured in the same manner as in the monitoring program for *Ecklonia* in the main study. Bicheno juveniles were measured in conjunction with other plants measured.

An entire year of measurements of *Ecklonia* juveniles was not possible at Bicheno despite bolstering the numbers with further plants from George III Reef in May 1988. Surviving juveniles at George III Reef were harvested in July 1989 for morphometric analysis similar to that for the *Ecklonia* harvested in the main study.

### *Macrocystis pyrifera*

Methods for *Macrocystis* were similar to those for *Ecklonia*. Fifteen plants were transplanted from Bicheno to George III Reef at George III Reef (B-G) on 9 July 1987 and controls established (G-G). Fifteen plants from George III Reef to Bicheno at Bicheno were outplanted 15 July 1987 (G-B) and controls established (B-B). The *Macrocystis* experiment was abandoned December 1987 at George III Reef and May 1988 at Bicheno when it became apparent that populations of transplants were going to be too difficult to maintain. This was due to the plants not being healthy due to conditions that were not suitable for *Macrocystis* generally on the east and south coasts

at that time and the plants were disappearing at a greater rate than it was possible to replace them. Up to these dates at the respective sites, the length and number of nodes of the longest frond were measured and the number of fronds per plant monitored on a regular basis.

### Statistics

Analysis of variance (ANOVA, Sokal and Rohlf 1969) were performed on the data to determine the statistical significance of differences between means.

## RESULTS

### *Ecklonia radiata*

#### Growth parameters

Increase in lamina length, total length and erosion rate of lamina for transplants is depicted in Figures 5.2-5.4. At George III Reef, while overall length remains similar for the period of the study, rates of length increment and erosion differed for the *Ecklonia* plants from the two sites.

Total length of the B-G plants and the G-G plants at maturity were equivalent to the measured length of the local monitored *Ecklonia* plants at George III Reef (approx. 80 cm). Mature plants harvested at Bicheno as part of the main study had an average lamina length of 58 cms i.e. the Bicheno plants grew longer at George III Reef.

Mean growth increment for similar periods of study is  $0.31 \pm .03$  cm/day for the B-G plants and  $0.30 \pm .04$  cm/day for the G-G plants. The growth increment in B-G plants does not vary seasonally as much as the local plants (G-G). G-G plants show a strong decline in growth rate in mid-summer-autumn and a large increase in winter-spring. Rates of erosion are the reverse situation, with large variations in rate for the B-G plants

compared to G-G plants. Erosion rates for B-G plants peaked in late summer-autumn while the minima were in spring .

Mean mature plant stipe length of B-G plants was longer than G-G plants (Fig. 5.5). The two different means approach their parent population means (George III Reef; 8-10 cm and Bicheno; 12-19 cm) for mature plants.

Peaks in the fertility index (Fig. 5.6) preceded peaks in erosion. Plants were most fertile in the winter, this concurred with the results for *Ecklonia* in the main part of the study.

Timing of seasonal changes in the B-G individuals was later than the G-G individuals for all monitored aspects.

Weight distribution along the length of the laminas of the transplants (Fig. 5.7), shows a peak at the 10-15 cm mark and a gradual decrease for the G-G plants, while the B-G plants have a peak at the 15-20 cm mark with a greater rate of decrease along the length of the lamina.

Unfortunately, there is not sufficient data to calculate the relative annual productivities as biomass variation is required for the summer period at least.

Results of the transplants to Bicheno, while not as conclusive due to loss as a result of adverse conditions at the site, indicate at least that the George III Reef (G-G) plants are not as suited to the environment, resulting in a higher rate of mortality.

### Fertility index

The Fertility Index of the transplants indicates that the majority of the plants became fertile within twelve months at George III Reef (Fig. 5.6). At Bicheno, the B-B plants were also found to be fertile within one year of transplant. The G-B plants however all disappeared less than twelve months from initiation and were not fertile when observed ten months

after initiation. Change in fertility status precedes change in erosion rate, so presumably once fertile, the tissue quickly erodes as spores are released.

### Macrocystis pyrifera

#### Growth parameters

Change in length of the longest frond, change in number of nodes of the longest frond and change in the number of fronds for the *Macrocystis* transplants at Bicheno are depicted in Figures 5.9-5.11. They demonstrated a steady growth of the plants until wiped out in 1988. Frond increment per month appears reduced in late summer.

## DISCUSSION

### Ecklonia

The length of the B-G stipes at George III Reef is close to that measured on plants from the parental population at Bicheno. As a consequence, these plants must have an inherent capacity for longer stipes. This is the first indication that stipe length is a genetic character rather than environmentally induced in *Ecklonia radiata*. Further studies however should use plants grown from gametophytes under similar situations to remove any doubt of the sporophytes inheriting characteristics as a result of preconditioning. Total length of the lamina however is environmentally induced, as total lengths are very similar for transplants of different parental stock.

The differences in the weight per segment along the length of the plants may be interpreted on the basis of a greater density of laterals on the B-G plants. These appear to erode more quickly than the central, thicker lamina region which makes up a greater portion of the biomass of the G-G plants. As a consequence, although the biomass per unit length is not as low

as the Bicheno plants originally, a higher weight per unit length is maintained for a longer part of the lamina. For plants harvested in the summer at both the sites in the near vicinity of on-going monitored plants (see '*Ecklonia*' chapter), the number of lamina was recorded for the mature part of the blade ie. after full width had been attained and the distance measured. Lateral densities could thus be calculated and the same was done for the juveniles harvested in winter at George III Reef. The results are presented in the following table:

TABLE 5.1 Table showing mean lateral width of harvested adult plants and harvested adult transplants.

	Lateral width(cm)	s.e	n.
<u>Summer</u>			
Bicheno	2.96	0.19	28
George III Reef	3.83	0.21	22
<u>Winter</u>			
B-G Juv.s	1.67	0.10	9
G-G Juv.s	2.06	0.11	5

The densities of the laterals harvested from the two different sites in the summer are significantly different (ANOVA,  $p=0.05$ ) and the evidence is strong to suggest that this is genetically determined as the character appears to be expressed when progeny of both sources are grown under similar conditions. Unfortunately, there were not enough juveniles to make the discrimination between the two parental types at the 0.05 level when grown under similar conditions (Figs 5.12 + 5.13).

The greater density of laterals on the Bicheno plants may be a response to high water movement situations. The concentration of the lamina surface area into a more confined region, close to the meristem and the top of the stipe may reduce drag. Plants with a greater proportion of the

lamina area in the central portion of the lamina rather than the laterals would have increased drag and be not be as suitable for high surge areas.

Plants at Bicheno appeared to display more corrugations and spines on the blade (see also Fig. 5.13). Features of rugosity and number of spines have also been noted to increase in *Macrocystis integrifolia* toward more exposed areas. This could be interpreted as a morphological feature to enhance nutrient uptake in calm waters, as they serve to break up the surface boundary layer by inducing turbulence. In rough water however, they may also increase strength (Norton *et al.* 1981, Lobban *et al.* 1985).

The differing patterns of growth of B-G and G-G plants displayed by length increment may be explained in terms of the differing temperature/nutrient regimes at the two sites. The Bicheno plants, accustomed to lower nutrient situations (and associated higher temperatures), may not be as nutrient-limited at George III Reef as the local plants. This results in less variation of the growth increment throughout the seasons.

How directly comparable the rates in lamina increase are may be in question however. The B-G plants are placing more effort into the production of laterals and thus may be expected to show differing lamina length increments and comparison of lamina increment may not be a strict comparison of productivities.

The high rate of erosion of the B-B plants after the spring-summer burst may be due to the less 'massive' central lamina in these plants resulting in a rapid degeneration after formation. The erosion rate of the G-G plants is much less variable.

Mortality rates of the transplants at Bicheno are much greater than those from either Bicheno or George III Reef. This is due to the adverse conditions they were exposed to early in their development. The mortality



rates for the George III Reef transplants however is comparable to the monitored plants at George III Reef.

Bicheno plants differ from George III Reef plants in having longer stipes and possibly higher density of laterals, are more spinuous and more corrugated. They appear adapted to a low nutrient-higher temperature environment. *Ecklonia radiata* demonstrates a high degree of morphological variability worldwide. These experiments are the first to discriminate between some genetic and environmentally induced characters.

### Macrocystis

Final growth values for the fronds of length increment and increment in number of blades are 1/3-1/2 the values measured on the monitored mature plants concurrently. Clendenning (1971) noted that initial fronds rarely reached the surface. The reduced growth rates of the initial fronds measured here may thus be due to the age of the fronds and their approaching demise. Some of the fronds observed were not healthy. Increase in rate of growth in the fronds is consistent with the s-shaped curve of growth rate, with growth rate becoming rapid after they had reached 50-80 cm long or 17-20 nodes.

Increase in the number of fronds compares with values measured by Zimmerman & Kremer (1986) at Santa Catalina Is. of 2-9 fronds per month and Gerard (1976), 2-14 fronds per month, increasing with plant size at Monterey Bay, California. Zimmerman & Kremer (1986) correlated frond increase to nitrate levels in the water and the result at Bicheno would appear to support this with a decrease in frond increment in late summer when temperatures are high are nitrate levels are low (Figs 2.10 and 2.19).

Calculating the age of *Macrocystis* plants from the number of fronds is tenuous because fronds die off where new fronds are being produced.

Gerard (1976) found that despite larger plants producing more fronds, they also lost more fronds on a monthly basis; therefore, the mean net addition rate of fronds was relatively constant for all plant sizes. Plants of up to 50 fronds had a net monthly increase of 1-2 fronds and larger plants of up to 70 fronds increased by 3-5 fronds each month. Plants here show similar results of approximately 2 fronds/month. Plants at Maria Island, where the number stipes were counted on a few plants, commonly had in the vicinity of 20 stipes. Such plants may be expected to be at least 12 months old.

## SUMMARY

### *Ecklonia*

When grown under similar conditions, *Ecklonia* plants from Bicheno and George III Reef show differences in morphology and response to environmental conditions indicating genetic differences. Bicheno plants have a capacity for longer stipes, less mass in the central lamina and potentially higher lateral densities. Plants grew to similar lengths so this factor is environmentally induced.

Lamina increment rates of George III Reef plants at George III Reef, showed a marked periodicity and a slightly differing timing compared to Bicheno plants grown at the same site. Differences may be attributed to the differing morphologies of the parental stocks and/or differing physiological adaptations.

In contrast, erosion rates of the Bicheno plants shows marked periodicity in comparison to George III Reef plants, with a high in autumn and a low in spring. Again differences may be ascribed to the differing morphologies of the parental stocks or may reflect differing physiological adaptations.

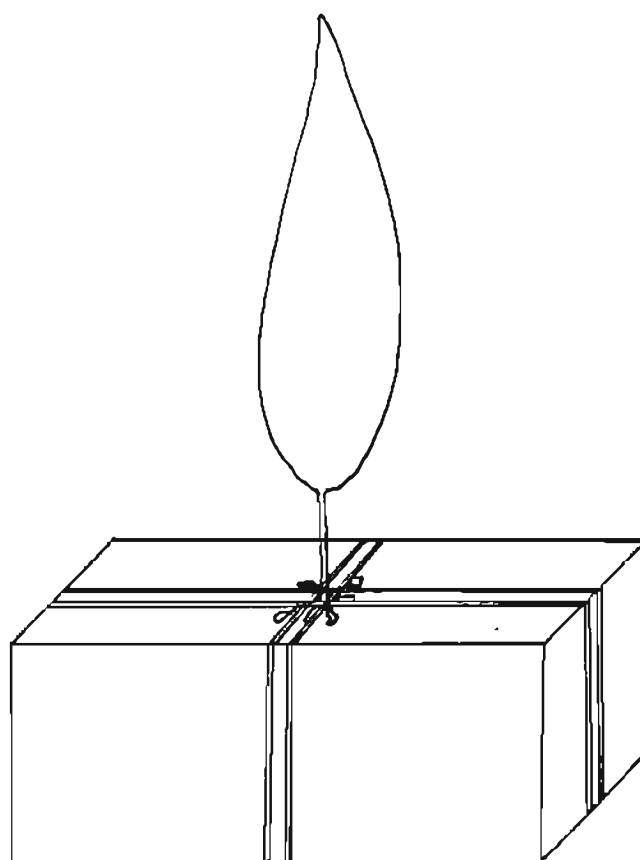
Plants at either site are able to reproduce at one year of age.

### Macrocystis

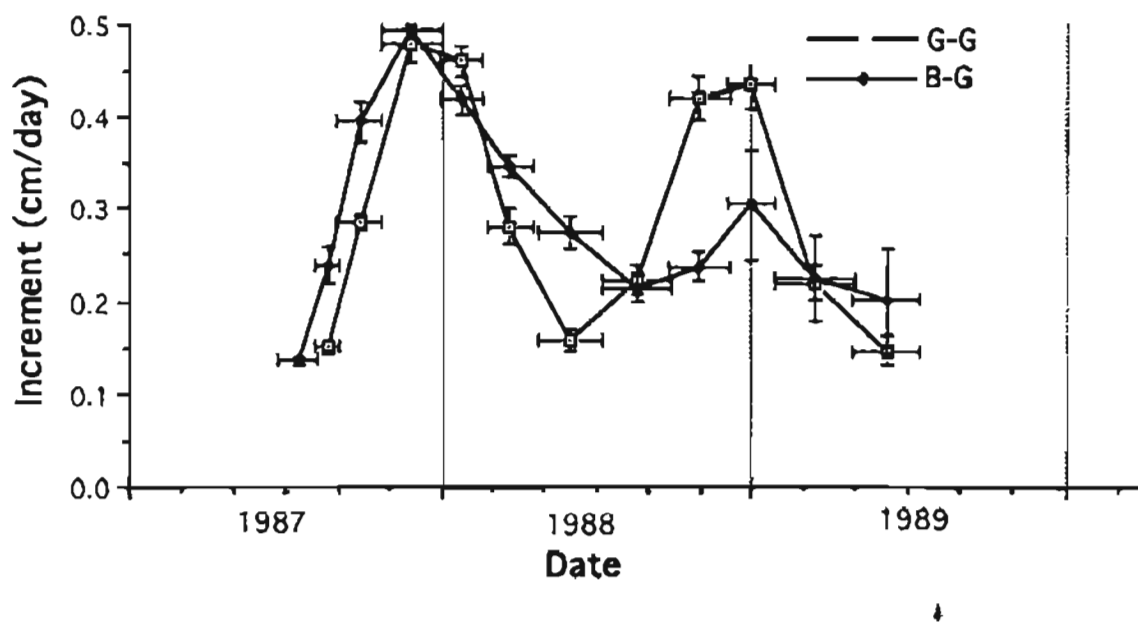
After eight months, plants at Bicheno were showing lower growth rates than more mature plants in the same area.

Increase in rate of growth in the fronds is consistent with the s-shaped curve of growth rate, with growth rate becoming rapid after they had reached 50-80 cm long or 17-20 nodes.

**Fig.5.1** Juveniles were attached to housebricks by rubber bands overlocking over the holdfast-haptera.



**Fig. 5.2 a)** Graph showing increment in lamina length for *Ecklonia* juveniles at George III Reef. **B-G**; Bicheno-George III Reef and **G-G**; George III Reef-George III Reef for 1987-1989.



**Fig. 5.2 b)** Graph showing increment in lamina length for *Ecklonia* transplants at Bicheno. **B-B**; Bicheno-Bicheno and **G-B**; George III Reef-Bicheno for 1987-1989.

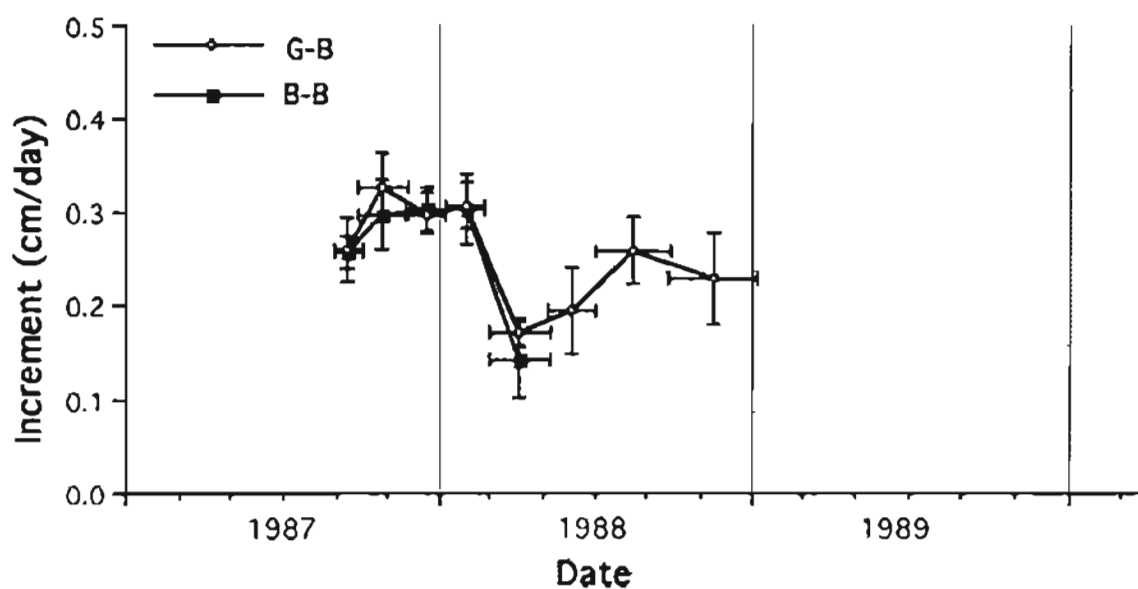
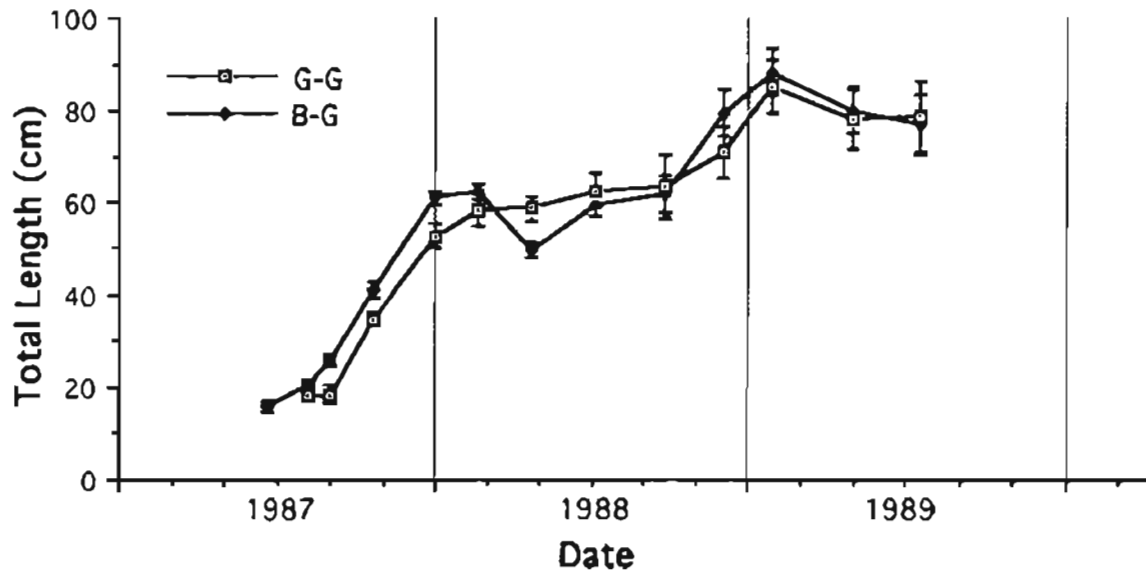


Fig. 5.3 Graph of total length of *Ecklonia* transplants.

a) George III Reef



b) Bicheno.

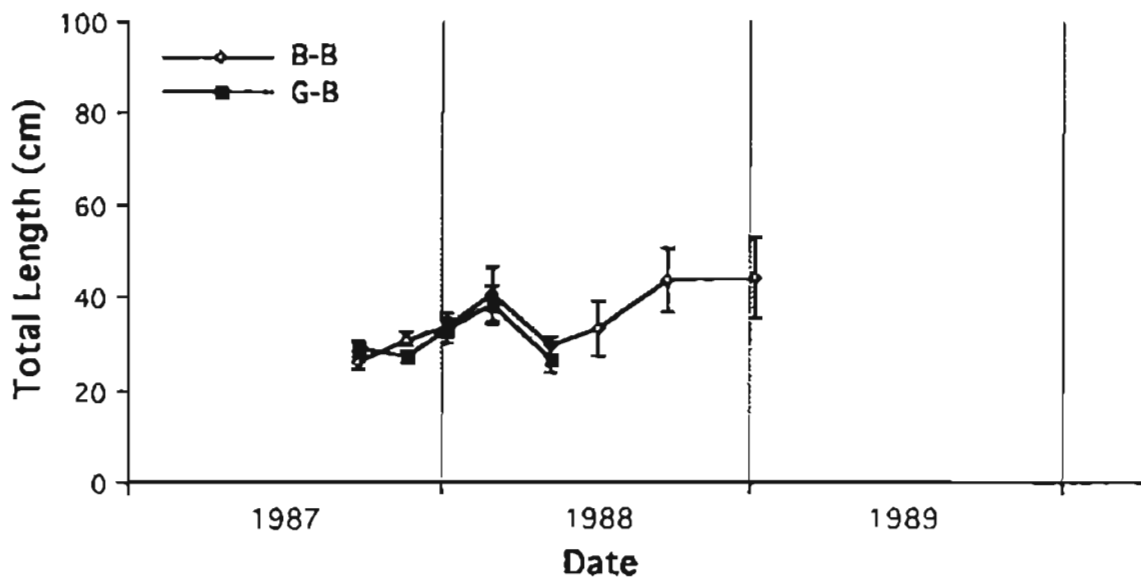
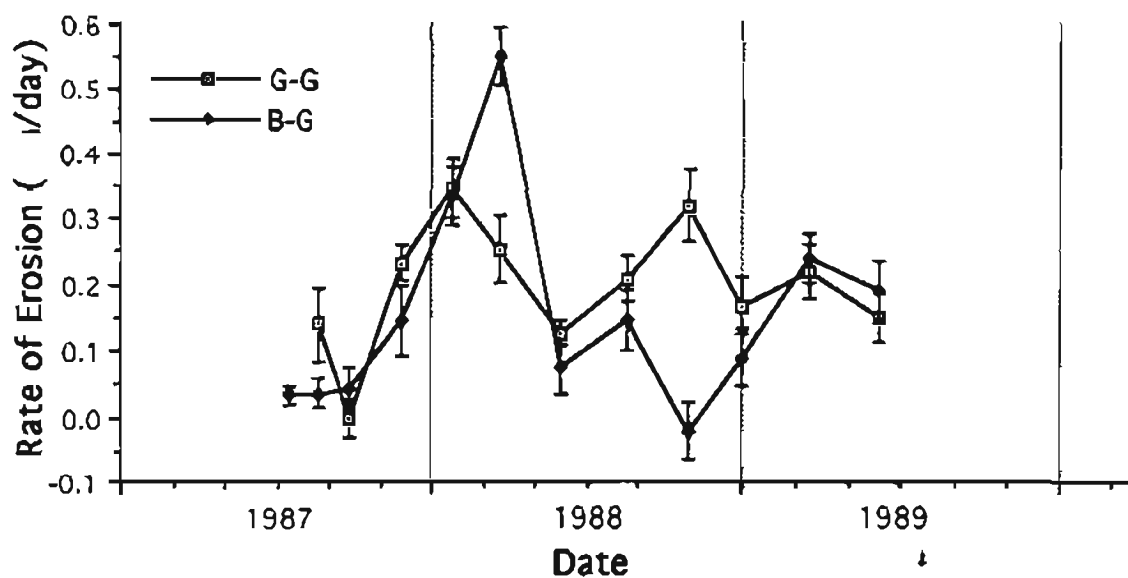


Fig. 5.4 Graph of rate of erosion for *Ecklonia* transplants.

a) George III Reef



b) Bicheno.

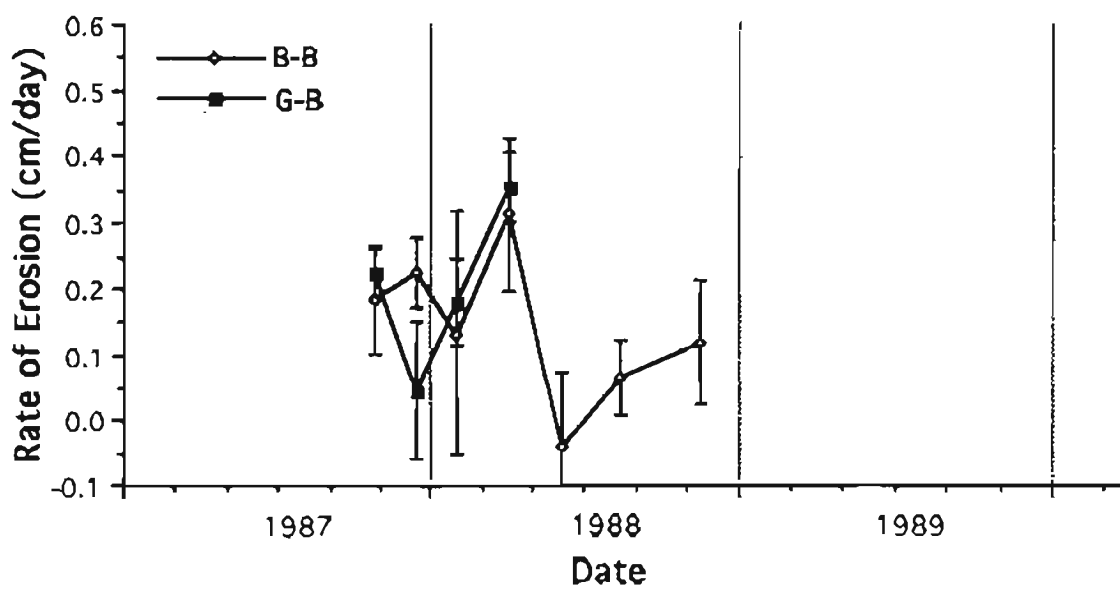
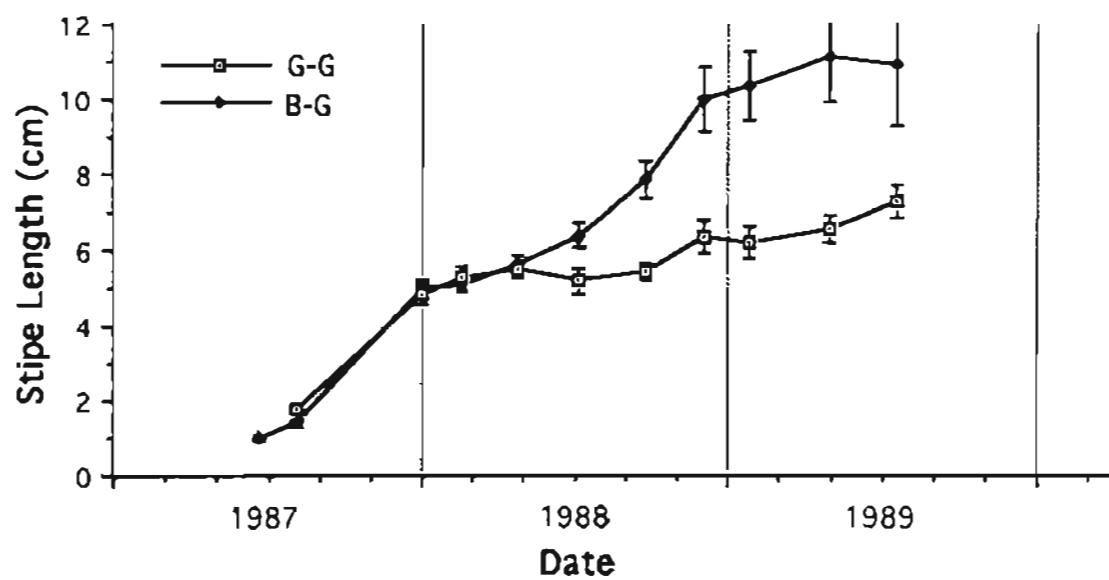


Fig. 5.5 Graph of stipe length of *Ecklonia* transplants.

a) George III Reef



b) Bicheno.

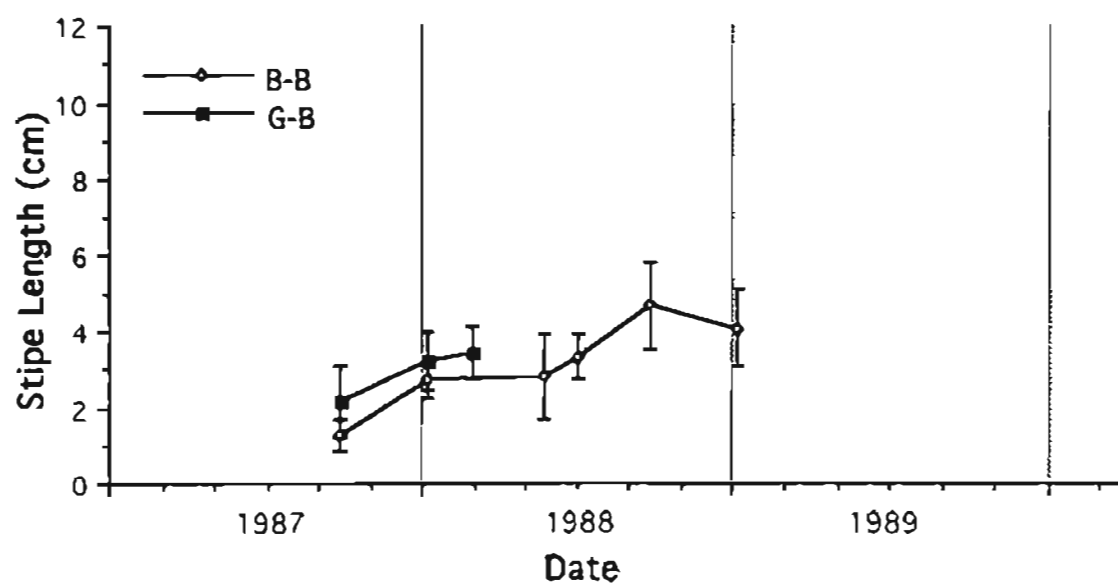




Fig. 5.6 Sexual Index for *Ecklonia* transplants at George III Reef.

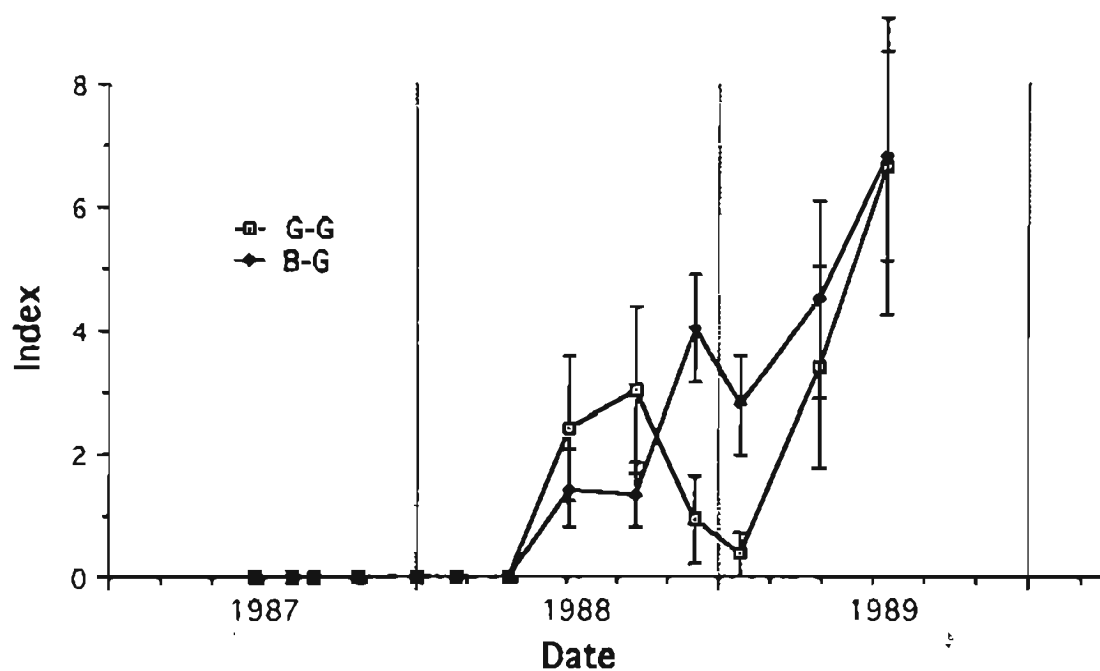


Fig. 5.7 Graph of weight per 5 cm segment from the base of the lamina to the eroding tip for *Ecklonia* transplants at George III Reef.

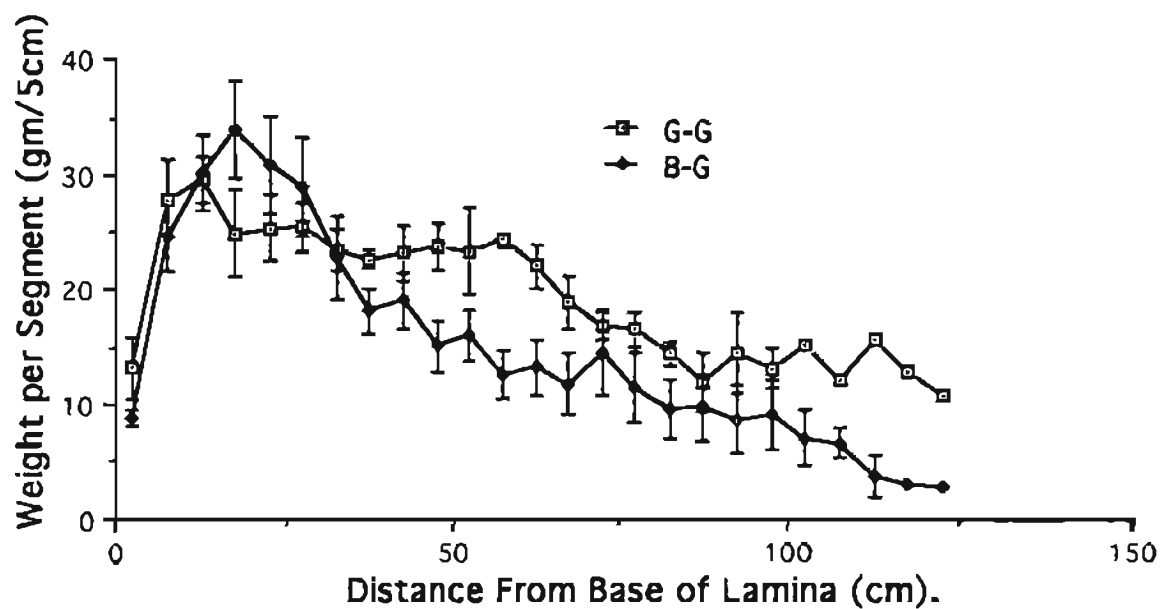
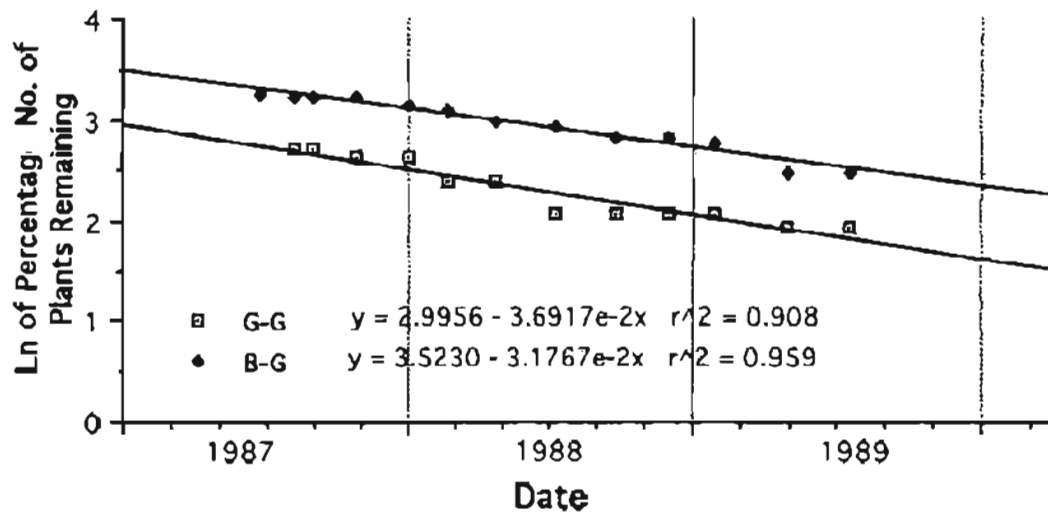


Fig. 5.8 Graph of natural log of percentage of number of *Ecklonia* transplants remaining of original number versus time or 'depletion curves'.

a) George III Reef



b) Bicheno

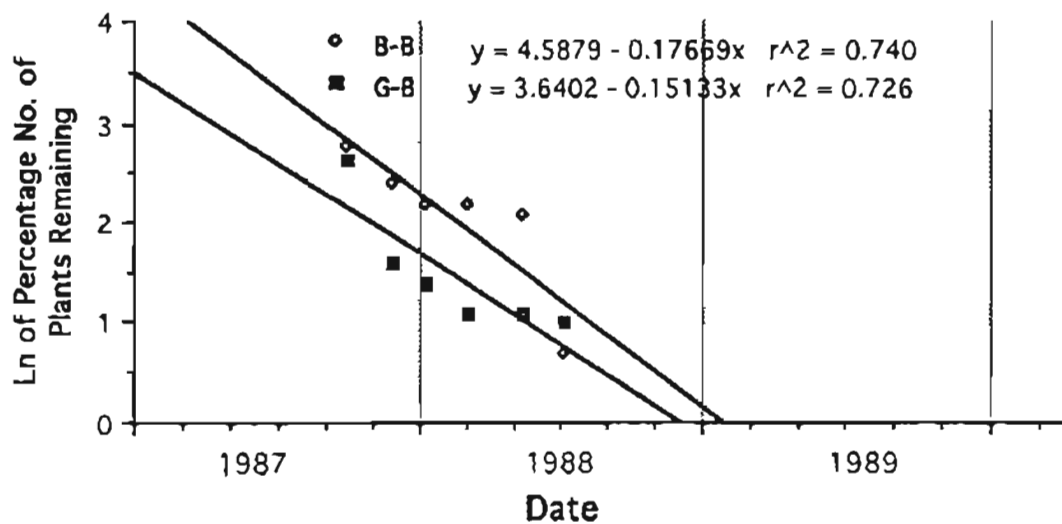


Fig 5.9 Graph showing the number of blades of longest frond for *Macrocystis* transplants at Bicheno, 1987-1988.

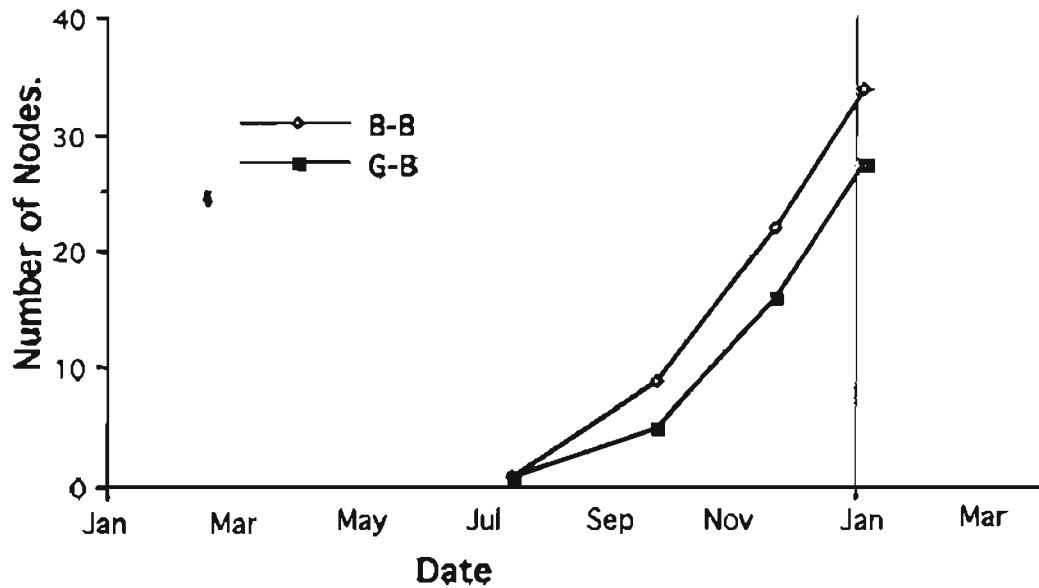


Fig. 5.10 Graph showing length of longest frond for *Macrocystis* transplants at Bicheno.

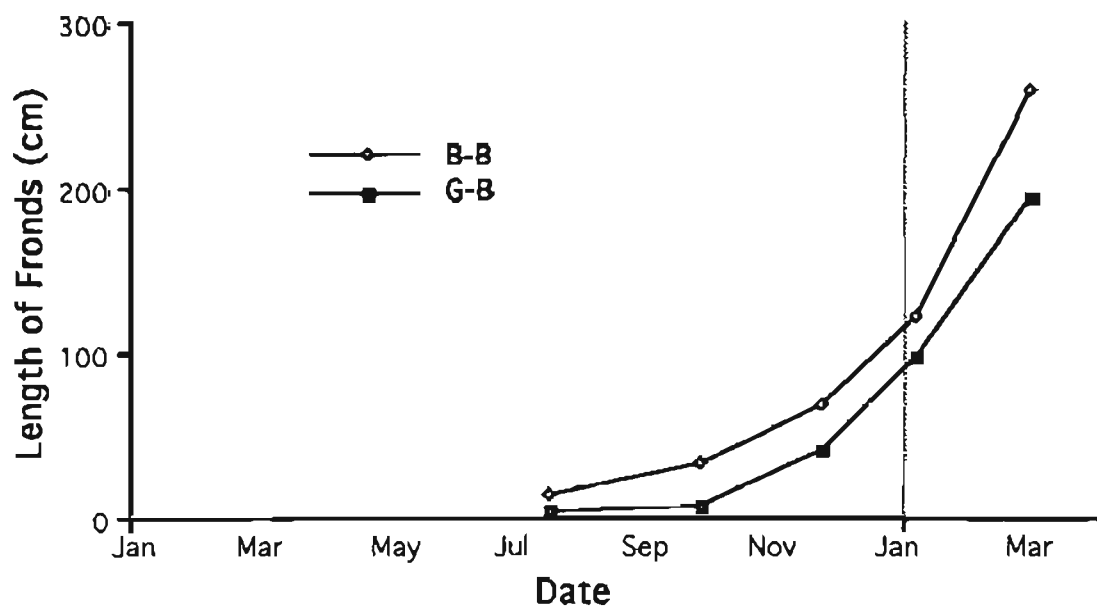
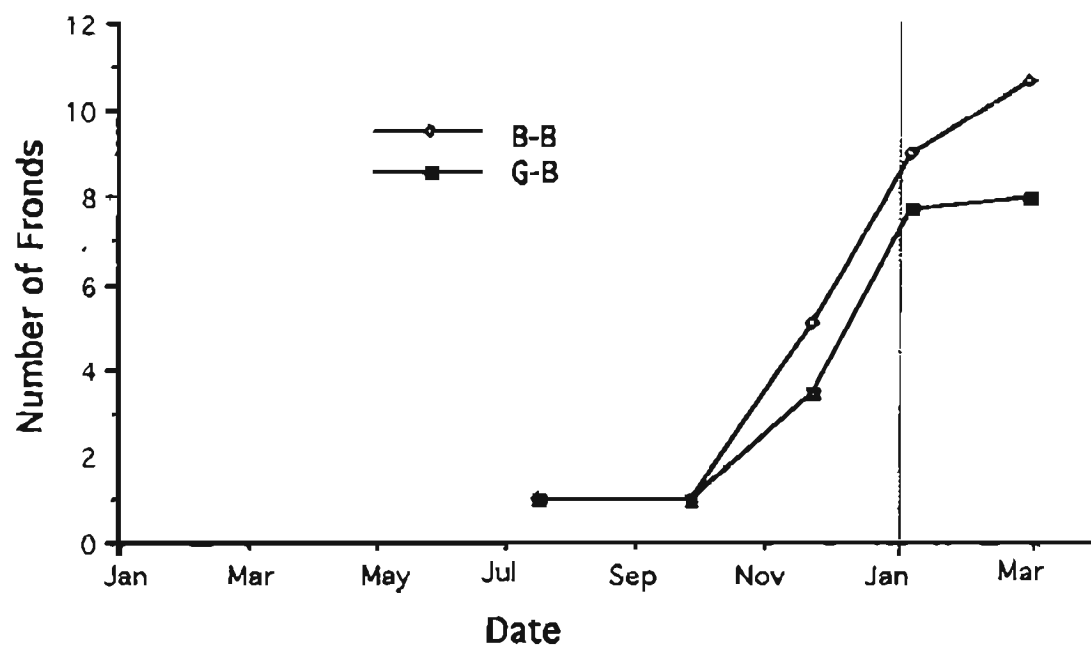


Fig. 5.11 Graph showing number of fronds for *Macrocystis* transplants at Bicheno.



LEGEND for figs 5.12 and 5.13, depicted on the following two pages, numbers 149 and 150.

**Fig. 5.12 a) and b)** Plants harvested two years after transplantation from George III Reef to George III Reef (G-G), **c) and d)** two plants harvested two years after transplantation from Bicheno to George III Reef (B-G).

**Fig. 5.13 a)** Mature plant harvested from George III Reef. Still has a sheep ear tag fastened with an electrical cable tie around the stipe, **b)**, **c) and d)** mature plants harvested from Bicheno. **c)** is an example of a long stiped individual.



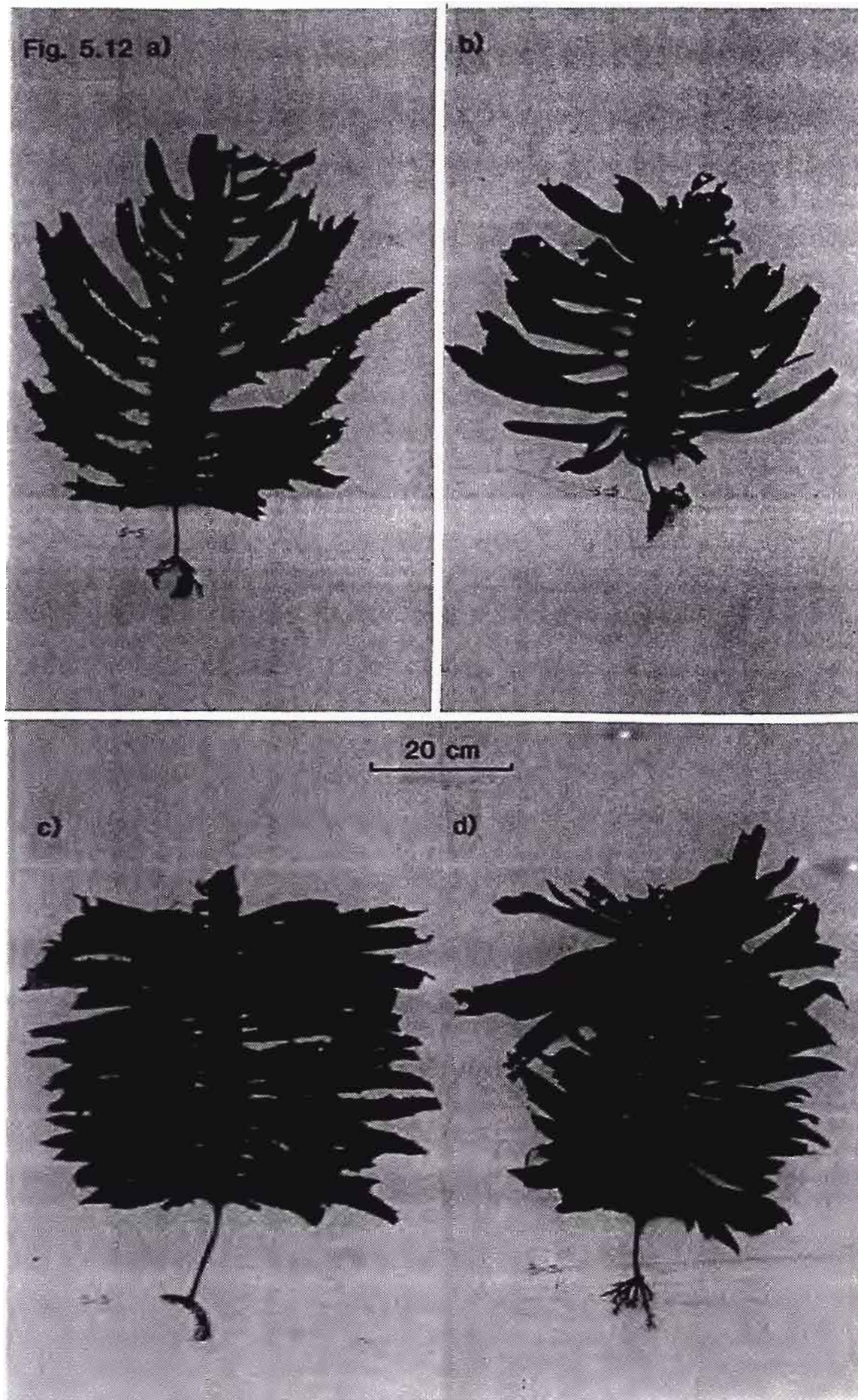


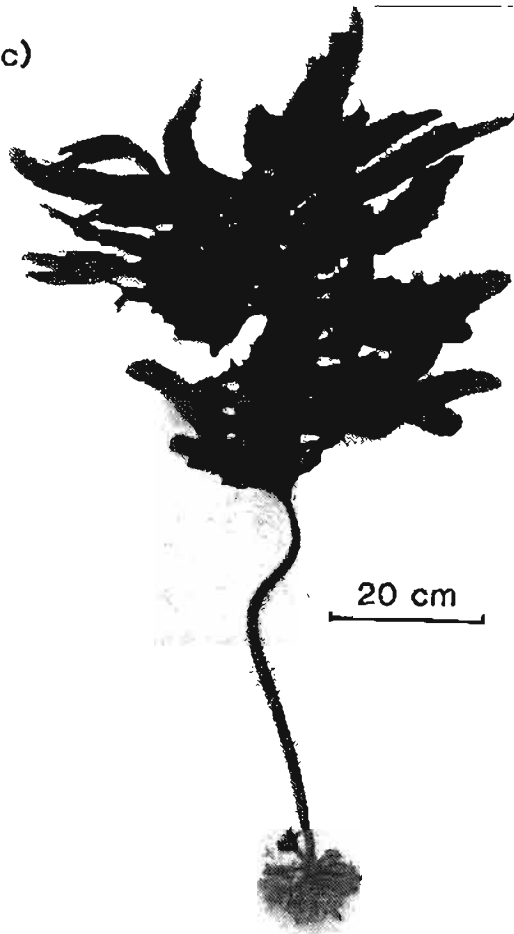
Fig. 5.13 a)



b)



c)



d)



## PART 2, CHAPTER 6.

### PHYLLOSPORA COMOSA

#### INTRODUCTION

*Phyllospora comosa* is one of the most abundant macroalgae on the southern Australian coastline and, as is the circumstance with most Australian macroalgae, few studies have been conducted beyond the taxonomic.

Unlike the previous two kelps investigated in this study, *Ecklonia radiata* and *Macrocystis pyrifera* which are members of the order Laminariales, *Phyllospora comosa* is a member of the Fucales. The distinguishing growth feature of the Fucales is growth from 1-4 apical cells, as distinct from the Laminariales where growth arises from an intercalary meristem.

There are few ecological studies of subtidal Furoids mainly because the group is best represented in the southern hemisphere and of the species that occur in the northern hemisphere, the greater majority are intertidal.

The thallus of *Phyllospora comosa* (Fig. 6.1) is dark brown and from 0.5-3 m long. It is much branched, with a short subterete stipe bearing primary branches. Normally, the initial branch forms the central main axis, from which secondary branches arise. If this is damaged, however, other lower order branches take over this function. The branches have simple marginal laterals closely arranged along their length, with scattered vesicles, all essentially in one plane but mostly displaced. The branch axes are 6-12 mm broad and 1-3 mm thick. Laterals are linear to slightly lanceolate, 5-16+ cm long and 3-12+ mm broad, occurring 1-2 mm apart, entire or with



occasional slight marginal spines. The vesicles are formed at the base of occasional laterals and are elongate to ovoid to broadly fusiform, usually apiculate or with a short apical leaflet, 2-4+ cm long and 0.5-2 cm in diameter and the wall; 1-3 mm thick. Growth is from a short series of four-sided apical cells in an apical depression (Womersley 1987).

External morphology and habit of this species is very similar to the western North American *Egregia menziesii* (a member of the Laminariales), an example perhaps of convergent evolution.

Womersley (1987) lists the distribution of *Phyllospora* from Robe, S. Australia, around Victoria and Tasmania to Port Macquarie, NSW. In Tasmania, *Phyllospora comosa* occurs and often dominates the rocky-reef substrate from 0 (Mean Low Water) to 6-10 m deep along the northern coastline and down to 18 m along the southern coastline. It is known commonly as 'cray weed' as it is often found on reef bottom suitable for crayfish.

Plants from the southern coastline tend to be larger than those from the north. At George III Reef, plants up to 15 kg were relatively common. The plant has a preference for rougher waters. On exposed coastlines it forms a band below the *Durvillaea potatorum* zone whereas in calmer waters it forms a narrow, virtually monospecific band (often < 1 m wide) in the surge zone. Plants in calmer waters are often subject to growth of epiphytes.

Tips of the branches of *Phyllospora comosa* often break off, and in late summer whole plants, branches and parts of branches are frequently observed floating on the ocean surface and cast up on the beach. These are from storm or surge damaged plants. Branches grow until the increasing stress from water motion acting over their entire length causes breakages. This appears more likely to happen after the spring 'burst' of growth and

towards late summer when a lessening of nutrients in the water appears likely to weaken the plants.

This plant was selected for growth studies due to its dominance at 6-8 m depth on George III Reef and its ubiquity in Tasmanian coastal waters. At Bicheno, *Phyllospora* is a prominent part of the flora from 2-10 m depth.

## METHOD

### Measurement of growth

As far as can be determined, there are no other in-situ studies of this plant within Australia. A method of determining growth of the plant was first established. Initially, plastic clothes tags were inserted (Fig. 6.2) with a tagging gun into the central portion of the branch at predetermined distances from the tips. Many branches broke at the point of insertion however. Surveyors tape, used for the *Macrocystis* was unsuitable due to the high water movement experienced by the ends of the branches of *Phyllospora comosa*, subsequently destroying the tape. Also, this tape did not allow accurate positioning on the branch. An alternative form of clothes tag was found that served the purpose adequately. This could be loosely secured around branches between laterals (Fig. 6.3) and did not appear to have any detrimental affect on the branch or the plant and movement up or down was prevented by the laterals.

To localize the area of greatest expansion on the branches, two tags were attached to each branch, the first approximately 10 cm from the tip and the second approximately 10-20 cm distant. The two distances were then measured underwater and recorded on a slate for later transcription in the laboratory. 'Living' and 'dead' branches were noted (see Fig. 6.1 c and d). A living branch was a branch that had its apex still intact. Dead branches ceased elongating.

After the first year, it was determined that extension in length of the branches was confined to the last 20-30 cm of the branches. From this time on, the entire branch was measured from its base and the branches identified by surveyors tape. Surveyors tape tied closely to the base of the branches, rather than towards the ends, lasted well (3-4 months), as it was more secure from water motion.

At George III Reef, *Phyllospora comosa* is present as a narrow band around the reef at 6-8 m depth. Fifteen plants were haphazardly chosen in the area of greatest concentration adjacent to the transect line at the 240 m mark.

Plants were identified by a plastic sheep tag secured to the stipe of the plant with a loosely attached plastic electrical tie. This did not seem to adversely affect the plants in any way and no tags were lost, save when entire plants disappeared. Branches were retagged on a regular basis to compensate for loss of the surveyors tape marking some of the branches and the death or loss of the growing tip of the branches.

Within plant variation of growth of branches was examined more closely at Bicheno. A relationship between length and growth increment is supported (see Fig. 6.5 b) for a session in mid - 1988. Analysis of tagging data however shows this relationship was not true for all sample sessions. Light (longer branches tended to be higher in the water column) or age of the laterals may be the determining factor. To ensure adequate coverage of the likely variability two branches always were tagged on each plant, one towards the base and the second near the top.

Sampling was done at intervals of approximately one month for the first year after which the sampling interval was approximately two months (overall mean; 54 days).

At Bicheno, a similar method was followed. Plants at Bicheno were selected on the basis of being close to stands of *Macrocystis* and *Ecklonia*

used in other parts of the study. All plant species studied were sampled at each session at Bicheno. Overall mean sampling period was 61 days.

#### Productivity determination

Detailed analysis of the productivity of *Phyllospora comosa* was beyond the scope of this project. An approximate estimate for George III plants for comparison with Bicheno and between other plants and areas was formulated. Values for the the number of living branches per unit area and the weight per unit length of the branches were required to convert growth increment determined to productivity per unit area. As these factors were likely to be seasonally variable, samples were taken mid-summer and mid-winter. Quadrats were harvested from an area subjectively determined as representative at both sites at the same depth as monitored plants. Quadrat size was large enough to include minor variations in density.

At George III Reef, in a monospecific stand of *Phyllospora comosa*, a 5 m x 5 m square quadrat was harvested in summer but as the logistics of collection of this amount of biomass proved difficult, only a 4 m x 4 m sample was taken in the winter. At Bicheno, a 5 m x 5 m quadrat was harvested in summer, and for similar reasons, a 4 m x 4 m, in the winter. This size quadrat was chosen as it was much larger than apparent within stand variation and so believed to be well representative of the community in the immediate vicinity. As there is only two quadrats harvested at each site, no variance is calculated. The Bicheno plants were harvested with associated *Ecklonia* plants (see Appendix 4). Retrospectively it would have been better to harvest 16 or 25 x 1 m<sup>2</sup> quadrats rather than one quadrat of 16 or 25 m<sup>2</sup>. This would have enabled an estimation of the variance in biomass distribution and so enable confidence levels for the production calculations.

Morphometrics of plants were analysed at the soonest possible time, this was within 24 hours of harvest. Care was taken to keep the plants cool

and moist. Each plant was weighed, the total number of branches counted and the proportion with intact apices (i.e. living) noted. A branch was cut off each plant, weighed and the length measured for an estimation of weight per unit length for calculation of biomass increase. A better means of determining annual biomass productivity of *Phyllospora comosa* would be to use the product of the increment and maximum biomass per unit length, similar to the method used for *Ecklonia* and *Macrocystis* (after Mann and Kirkman 1981, see chapter 4).

Biomass varied along the length of the branches, especially in the George III Reef plants. Towards the tips of the branches, there was a decrease in biomass with decreasing age of the laterals. Towards the base of the branches nearer the central axis there was a decrease in biomass with loss of laterals with age and erosion. A number of branches were harvested from *Phyllospora* at George III Reef on 4 November 1989 to determine the likely inherent error caused by the former method. Branches of a variety of lengths were cut into 5 cm sections, the number of laterals and the number of vesicles on each was determined and weighed.

Results as detailed in Chapter 2; The Coastal Environment, were used for regression against measured growth rates to determine likely limiting factors for this species growth at the two sites investigated.

### Statistics

Statistics used in this chapter are the same as those specified in Chapter 3 and 4.

## RESULTS

### Morphometric analysis

Simple morphometric relationships of plants harvested in November 1989 are presented in Figs 6.6-6.8. An increase in biomass per unit length corresponding to an increase in the density of the laterals for the first 30 cm of the branch from the apex is demonstrated (Figs 6.6 and 6.7) more so for the older-longer branches. Biomass is then relatively constant to the 90 centimetre mark after which it decreases. The lateral density decreases after the 60 centimetre mark however, indicating heavier laterals from 60 centimetres onwards.

Accumulating number of vesicles from the apex of the branches matches weight accumulation (Fig. 6.8 a). A good correlation is found for the total number of vesicles on a plant and its mass (Fig. 6.8 b,  $r = .97$ ,  $p = .0001$ ). The number of vesicles produced must be accurately determined by the plant for optimum buoyancy of the branches and in this instance, corresponds to one vesicle for every 5.8 g (wet weight) of plant material. The mechanisms for achieving this suggest a further possible study.

### Growth increment

Change in growth increment for *Phyllospora* at the two sites is demonstrated in Fig. 6.9. At George III Reef, there is a peak in growth November-January and troughs in May-June. In 1988, however, growth rates remained low for later in the year, until the termination of measurements in August. At Bicheno there were peaks from October to February, with a low in April. Average increment of branches from plants at George III Reef were  $1.34 \pm 0.05$  mm per day ( $n=259$ ), ranging for individual plants from near zero to a maximum of 3.6 mm per day over one period of 58 days. At Bicheno, rates were not quite so high with an average of  $0.93 \pm$

0.06 mm/day (n=111) with a maximum of 3.1 mm/day over one period of 43 days for an individual plant. One plant sampled in November 1989 at George III Reef had branches three metres long indicating an age of at least 6.1 years. Plants of this size and larger were common at George III Reef.

Regression of measured environmental parameters against growth rate of *Phyllospora* supports the premise of available light as the predominate factor affecting growth at both George III Reef and Bicheno. Equations best describing this are;

George III Reef;

→ Growth increment =  $0.033 + 0.018 \times \text{SUNSHG}$ ,  $r = .534$ ,  $p = .0007$ .

Bicheno;

→ Growth increment =  $-0.064 + 0.026 \times \text{SUNSHB}$ ,  $r = 0.855$ ,  $p = .0016$ .

Regressions can be improved if points are taken out that correspond to periods where temperature has averaged over 14.5° C ( $r = .85$ ,  $.94$ ,  $p = 0.0001$ ,  $.001$ , see Fig.s 6.10). Similar to the situation for the *Ecklonia*, growth is probably affected by low nutrient concentrations at these temperatures rather than the temperatures themselves.

### Lateral life span

Laterals develop on the branches from the apex back to the main axis. These peak in density at the 30 cm mark to the 90 cm mark on the few branches observed from George III Reef. Presumably the time from initiation to the 90 cm mark represents the maximum possible life of these leafy laterals. Assuming a growth rate as above, time from initiation to loss is 1.8 years. In this time, some bear conceptacles in which antheridia or oogonia develop. These are shed before the lateral also disappears.

### Plant lifespan

As for *Ecklonia*, depletion curves were fitted to the number of plants surviving through time (Fig. 6.11). These indicate half lives of 34.1 months at Georges and 26.4 months at Bicheno for the entire sampling period. Plants at George III Reef suffered no mortality for the first two years after which there was relatively fast plant loss. A depletion curve fitted to plant number for 1988 only, indicates a half life of only 6.4 months.

### Details of harvested plants and productivity estimates

The percentage of laterals dying between sampling periods is depicted in Fig. 6.12. Dying branches peak over the winter and might be considered an indication of the health of the plants. At George III Reef, similar to the mortality results, plant health as reflected in the mortality of the branches, appears good early in the study with a deterioration towards the latter. This was also noted for the *Macrocystis*. It is likely that the incidence of the EAC (East Australian Current) and the warm winter of 1988 may be responsible. Note the high mortality in the first sampling session, this also coincides with the incidence of the EAC in southern waters, March 1985 (Harris *et al.* 1991, Figs 2.9 a, 2.11).

A good fit for the number of live branches and the number of dead branches versus the weight of the plants is obtained from linear regressions (Figs 6.13 and 6.14). At George III Reef, a greater percentage of the branches are dead in the winter compared with the summer. The difference is not so marked at Bicheno.

Weight distribution of plants over 100 gm (excluding juveniles) for summer and winter harvested quadrats at both sites is depicted in Figure 6.15. They demonstrate two different populations at the two sites with larger plants at George III Reef.



Biomass per unit length of the branches of *Phyllospora* is presented in table 6.1. Mean branch length is obtained from total harvested plant weight divided by the mean weight per unit length and by the number of branches. At George III Reef the branches are heaviest per unit length in summer which contrasts with the results for the Bicheno plants which again present the opposite case. The smaller and lighter branches at George III Reef plants in summer is due probably to new branch initiation.

**TABLE 6.1** Biomass of fronds of *Phyllospora comosa* for George III Reef and Bicheno ( $\pm$  s.e).

	<u>Summer</u>			<u>Winter</u>		
	Mean Branch Wt/Length (g/cm.)	Mean. Branch Wt* (g.)	Mean Branch Length (cm.)	Mean Branch Wt/Length (g/cm)	Mean Branch Wt* (g.)	Mean Branch Length (cm.)
George III Reef	2.15 $\pm 0.11$	94 $\pm 6$	43.8 $\pm 5.1$	1.63 $\pm 0.09$	137 $\pm 15$	84.2 $\pm 13.7$
Bicheno	1.62 $\pm 0.15$	70 $\pm 5$	43.2 $\pm 9.9$	2.24 $\pm 0.09$	94 $\pm 5$	41.9 $\pm 3.97$

\* From total weight of harvested quadrat and the total number of branches.

Annual productivity per unit area of *Phyllospora* is calculated using; the mean weight per unit length, the mean number of live branches per unit area from summer and winter values and the mean branch increment for the period of the experiment (table 6.2).

Retrospectively, a value for maximum biomass per unit length as demonstrated in Fig. 6.6a would have been better for production calculations than the overall mean average biomass per unit length used. For the branches harvested on the 4 Nov 1989, a relationship could be determined for the length of the branch and the difference between the weight per unit length and the maximum biomass (see Fig. 6.16). Using the values for mean length in table 6.1 for each site and for summer and winter,

we can adjust our estimates of annual production (assuming constancy of the relationship over time and place). This gives an underestimation of

TABLE 6.2 Calculation of annual productivity for the harvested quadrats.

		Harv. Area (m <sup>2</sup> )	Harv. Wt. (kg)	Est. % cover	Wet Wt. /area (kg/m <sup>2</sup> )	Mean Incre (cm/day)	Live Branches No./kg	Branch Wt/L (g/cm)	Ann Prod /area (kg/m <sup>2</sup> )
George III Reef	S.	25	143.5	80	5.74	.134	8.3	2.15	5.05
	W.	16	120.4	70	7.53	.134	8.5	1.63	
Bicheno	S.	25	82	30	3.28	.093	10.8	1.62	1.48
	W.	16	21.9	15	1.37	.093	9.8	2.24	

branch weight of 68.7% at George III Reef and 74.0% at Bicheno. The adjusted value for production is thus 7.4 kg/m<sup>2</sup>/yr at George III Reef and 2.0 kg/m<sup>2</sup>/yr at Bicheno. Another possible source of error not considered may be extra biomass from the continued development of laterals by branches with dead tips.

## DISCUSSION

### Growth rates

The decline in growth at George III Reef in 1988, occurs simultaneously with the loss of plants where there had been no loss before hand. This also coincides with the incursion of the EAC, the warm winter and consequent reduction in available nutrients in the sea-water for this period. This could have weakened the plants and made them more susceptible to loss through wave action. Another possible explanation is

that initially, all plants were of the same cohort and have simultaneously reached a size too large to be held by the holdfast.

### Mortality

The indicated higher mortality of the plants at Bicheno is most likely due to the intermittent and higher wave climate these alga are subject to. A further influence may be the lower nutrient levels in conjunction with higher temperatures that seem to have had a deleterious effect on the George III Reef plants experienced with greater frequency in this area.

### Plant weight distribution

The weight distribution of plants harvested in the summer and the winter for plants at George III Reef is similar (Fig. 6.14). There appears to be peaks in the 100 g-1.99 kg and the 2-4 kg groups. The smaller plants may be subcanopy and stifled (for light). These may be ready to grow in the event of the loss of larger plants.

Bicheno plants are smaller overall than the George III Reef plants. This is probably a reflection of the greater depth (lower light) and higher mortality.

### Productivity

Cover of this alga at George III Reef is continuous and the calculated annual value of 7.4 (wet wt) kg/m<sup>2</sup>/yr is similar to comparable algae (Laminariales and Fucales) in similar niches. At Bicheno, the production of this alga must be combined with that calculated for *Ecklonia* (see *Ecklonia* chapter and relative percentages of both present). Together, they suggest a combined production of 4.8 kg (wet wt)/m<sup>2</sup>/yr in the quadrats harvested. The higher production at George III Reef would be due to the shallower waters although at Bicheno there is the potential to be more productive at

similar depths due to clearer waters. At Bicheno the higher mortality of plants of both species and the lower resultant densities may be a contributing factor.

These two algae constitute the perennial complement of the dominant algae at this depth at Bicheno, and the harvested quantities reflect actual species ratios at this depth. *Macrocystis pyrifera* can be present in large amounts, but distribution is patchy and spasmodic.

These estimates also do not take into account production due to all macroalgae at these sites. Encrusting coralline cover is often close to 100% in the lowest strata at Bicheno and George III Reef.

The calculated production at George III Reef of approximately 7.4 kg/m<sup>2</sup>/yr (at 7.7m depth) compares with the combined *Phyllospora comosa* and *Ecklonia radiata* annual production figure of 4.8 kg/m<sup>2</sup>/yr at Bicheno (10m depth). The higher production would be due to the shallower waters at George III Reef although at Bicheno there is the potential to be more productive at similar depths due to clearer waters. Other contributing factors are the higher mortality of plants at Bicheno and lower resultant densities.

## SUMMARY

Maximum biomass levels on the branches occurred between 30-90 cm from the apex. For the first 30 cm, the branch is still elongating, after 90 cm laterals are rapidly lost.

Mean daily increment of branches was  $1.34 \pm 0.05$  mm/day at George III Reef and  $0.93 \pm 0.06$  mm/day at Bicheno.

Mean growth rates of branches indicates a life expectancy of at least 6.1 years for plants at George III Reef.

Fig. 6.1 *Phyllospora comosa* habit photographs; a) mature plant b) young plant c) 'live' tip of branch and d) 'dead' tip of branch.



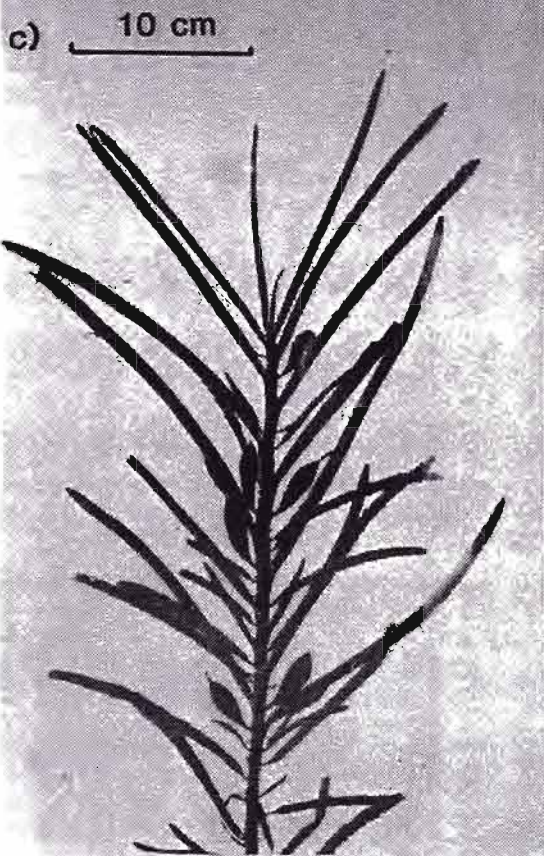
Fig. 6.1 a)



b)



c)



d)

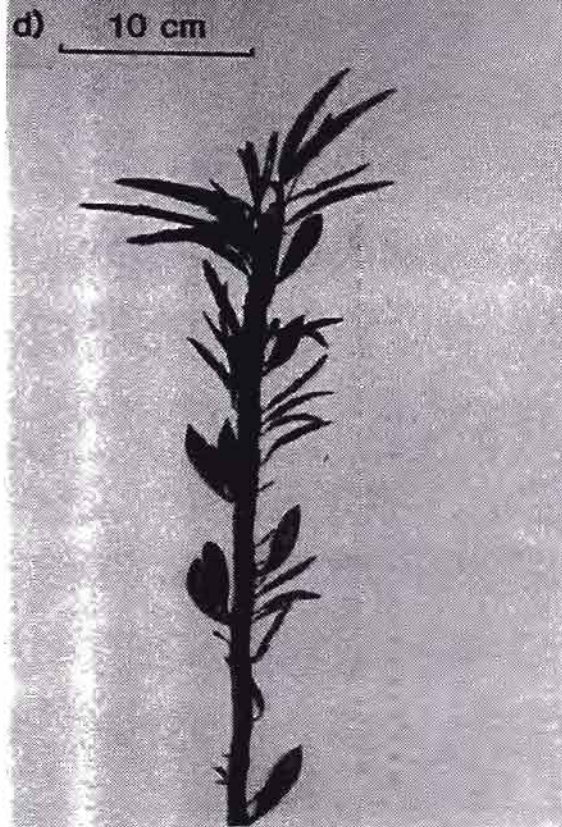




Fig. 6.2 Cloths tag-1 through central axis of branch.

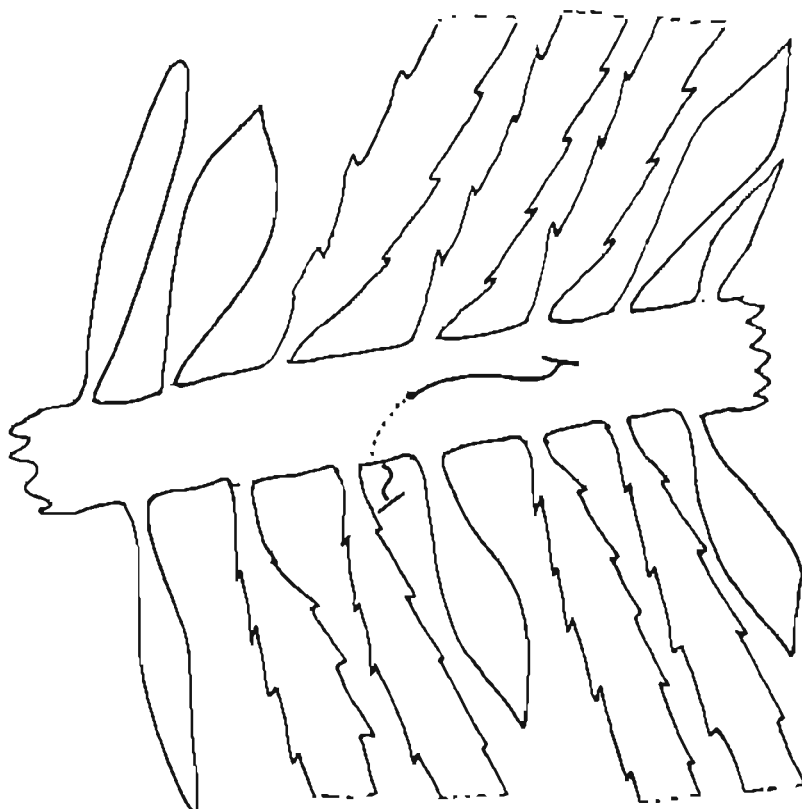
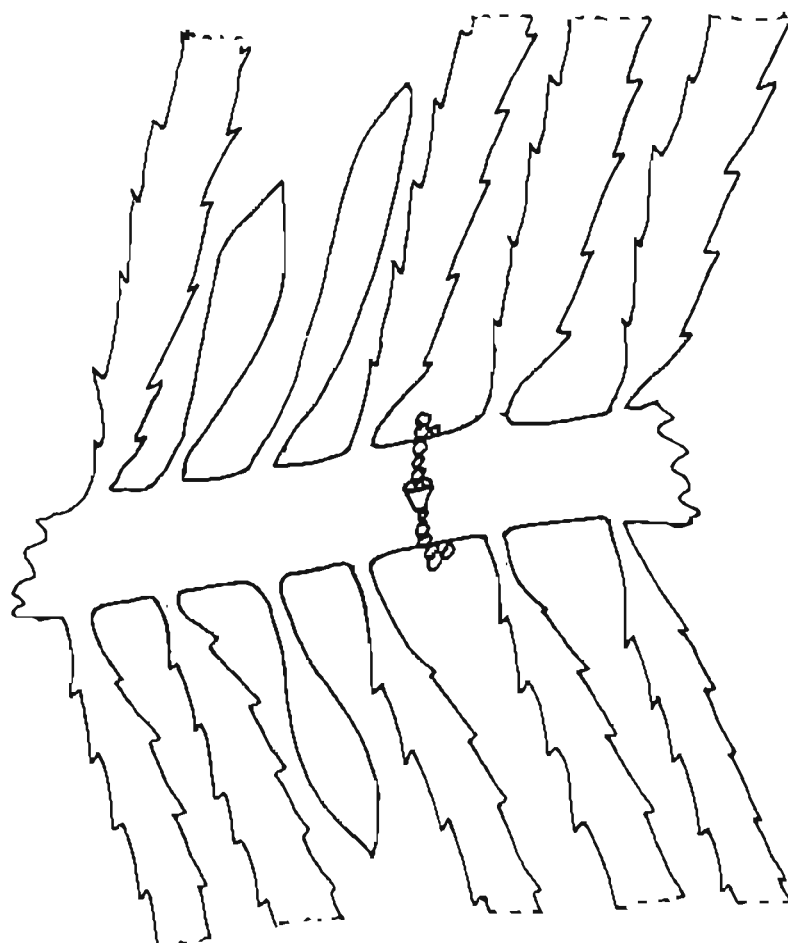


Fig. 6.3 Cloths tag-2 around *Phyllospora* branch between laterals.



**Fig. 6.4** Graph of growth increment versus the initial length of the branch for the period 2 July '88 to 24 Sept. '88 for *Phyllospora* plants at Bicheno.

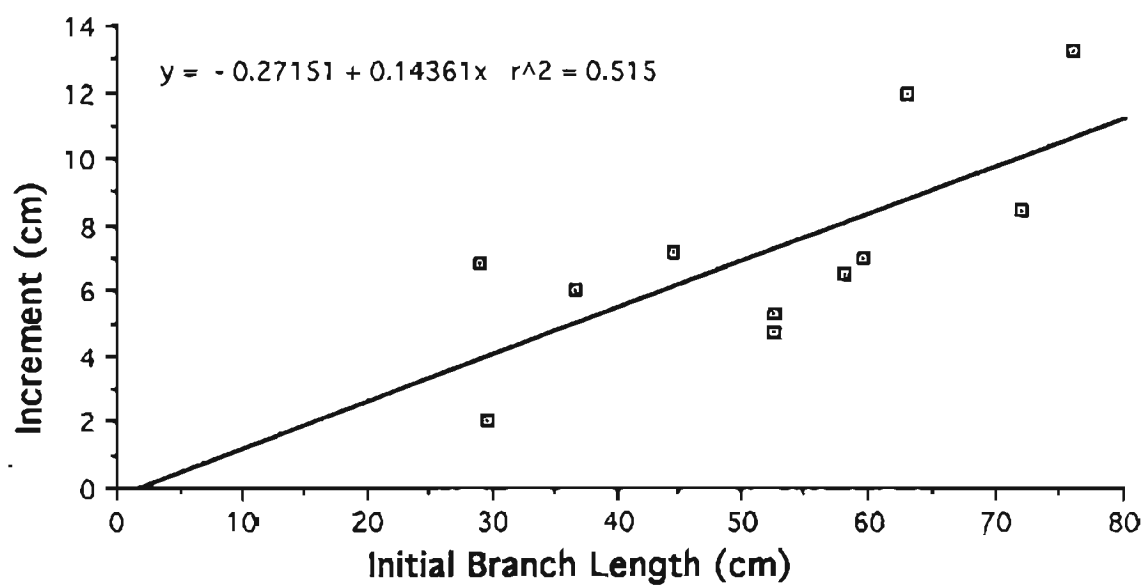




Fig. 6.5 a) Weight of 5 cm segments numbering away from the apex for branches of differing sizes. Harvested 4 Nov. 1989, George III Reef.

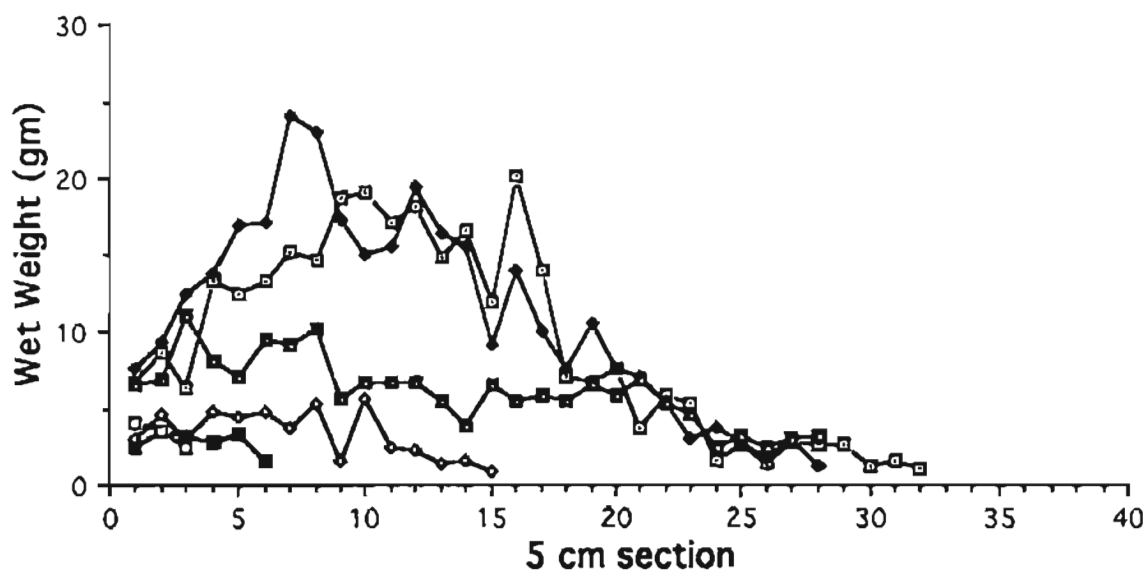


Fig. 6.5 b) Accumulating weight for segments numbering away from the apex from branches of differing sizes.

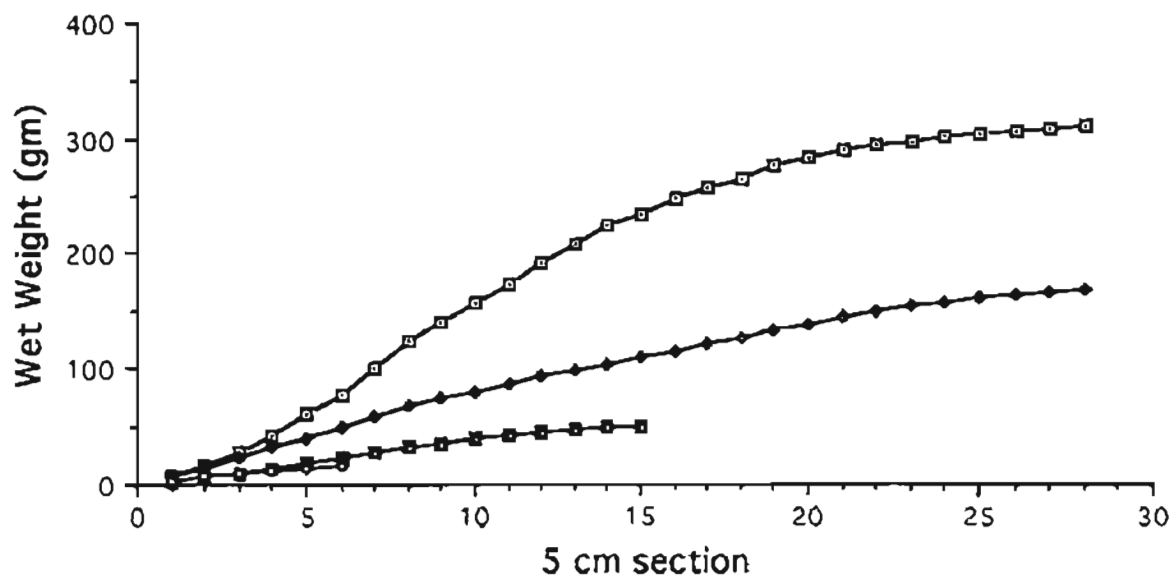


Fig. 6.6 a) Number of laterals per 5 cm segment numbering away from the apex for branches of differing sizes. Harvested 4 Nov. 1989, George III Reef.

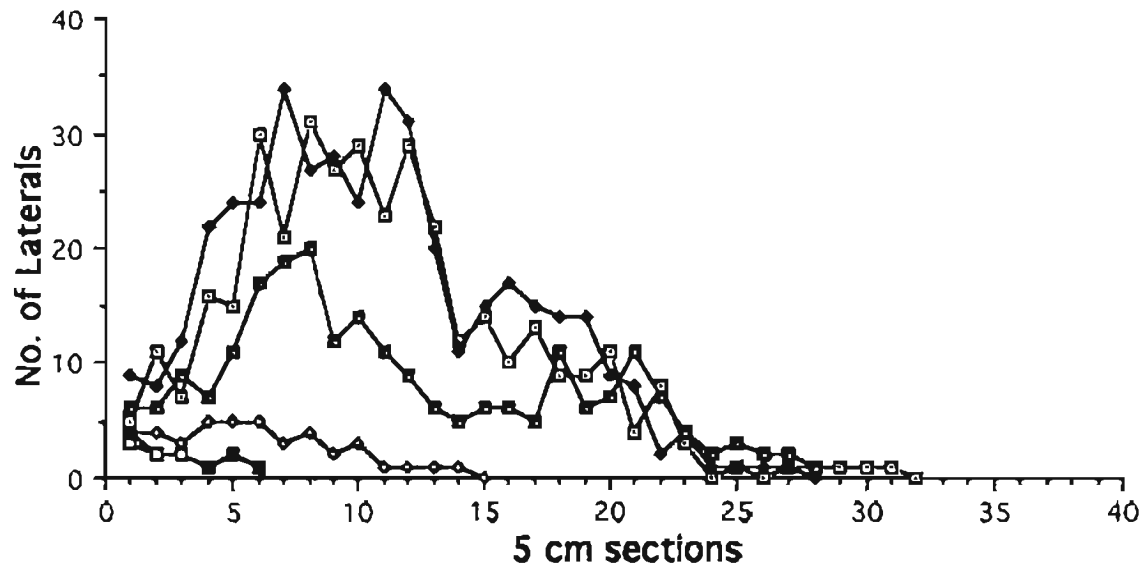


Fig. 6.6 b) Accumulating number of laterals for segments numbering away from the apex for branches of differing sizes.

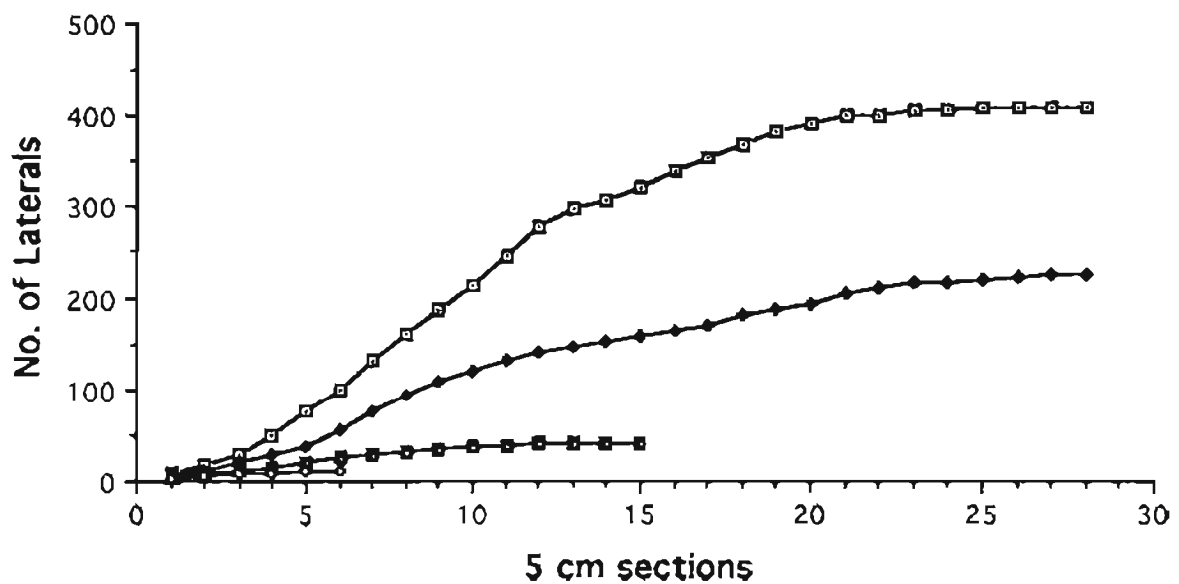


Fig. 6.7 a) Accumulating number of vesicles for segments numbering away from the apex for branches of differing sizes. Harvested 4 Nov. 1989, George III Reef.

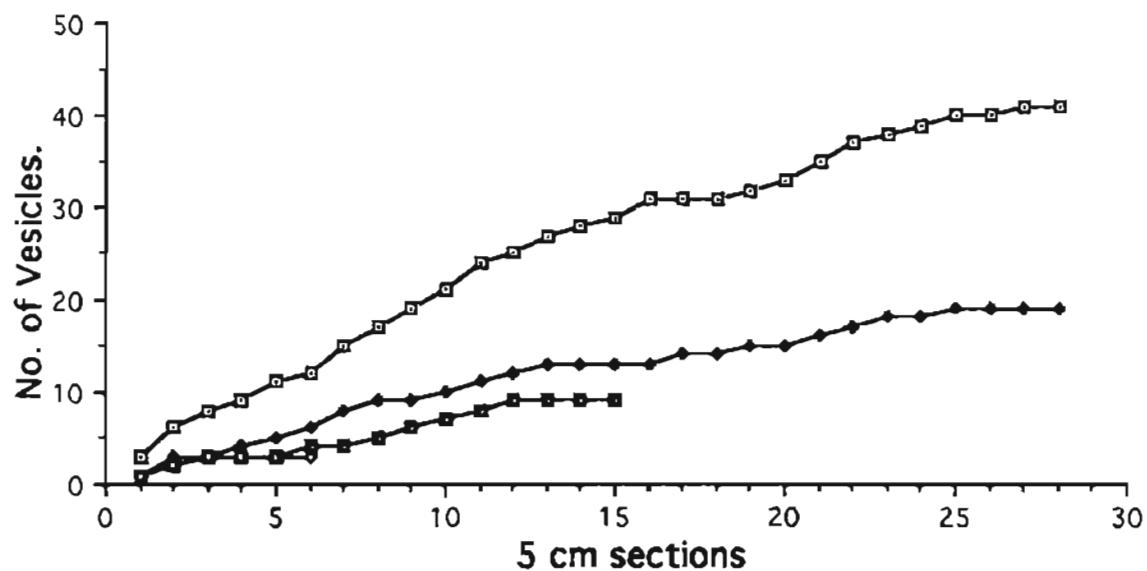
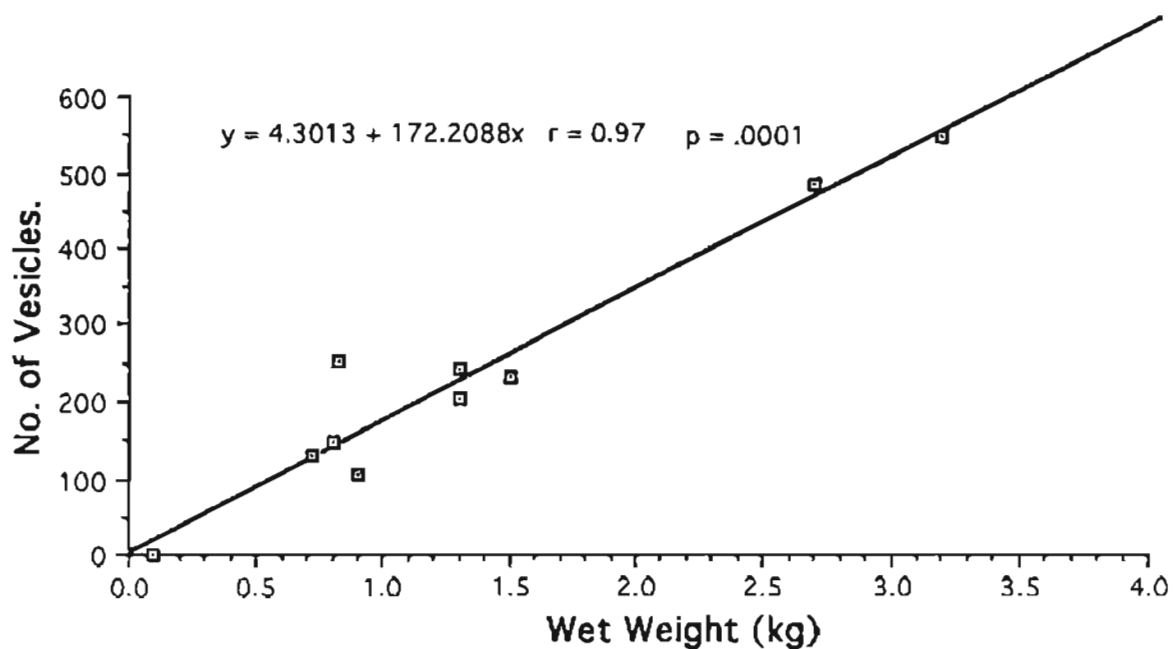
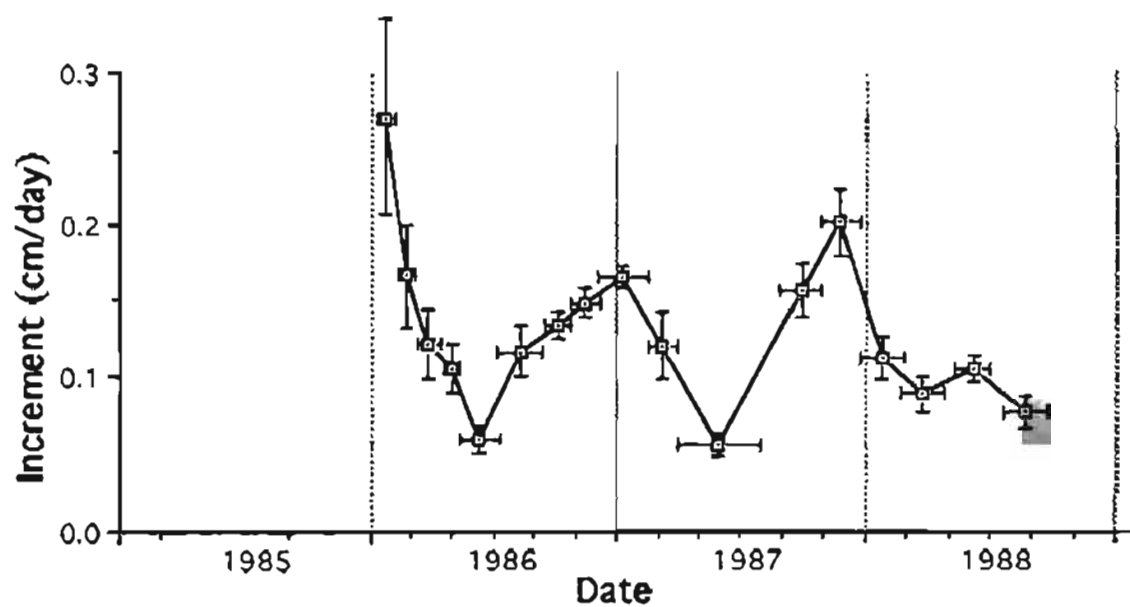


Fig. 6.7 b) Number of vesicles versus plant weight for *Phyllospora* plants collected off Southport Island on November 1985.



**Fig. 6.8** Increment in branch length. Vertical bars are standard error, horizontal bars are sampling period.

**a) George III Reef.**



**b) Bicheno**

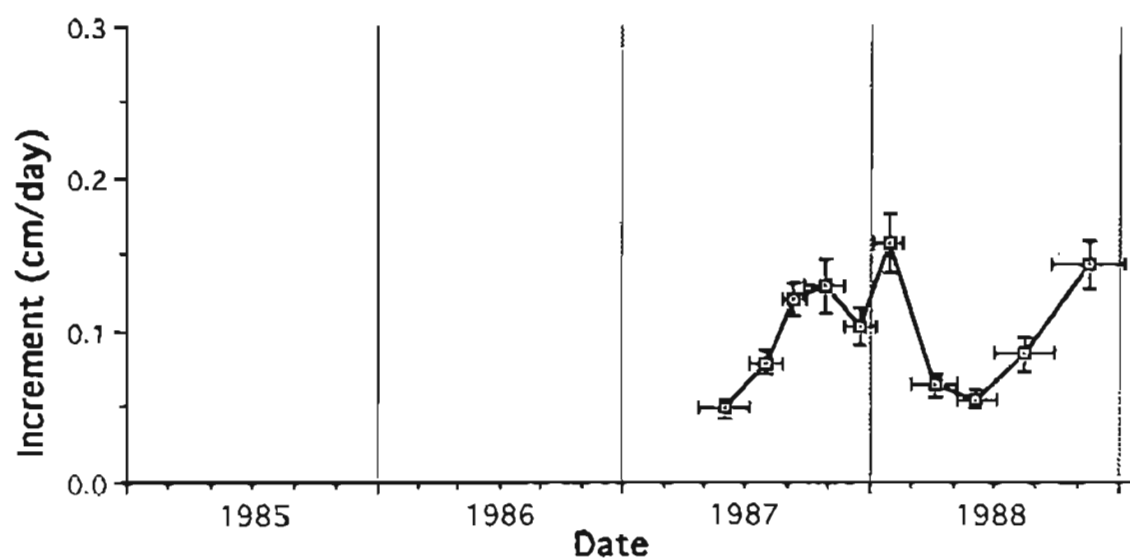
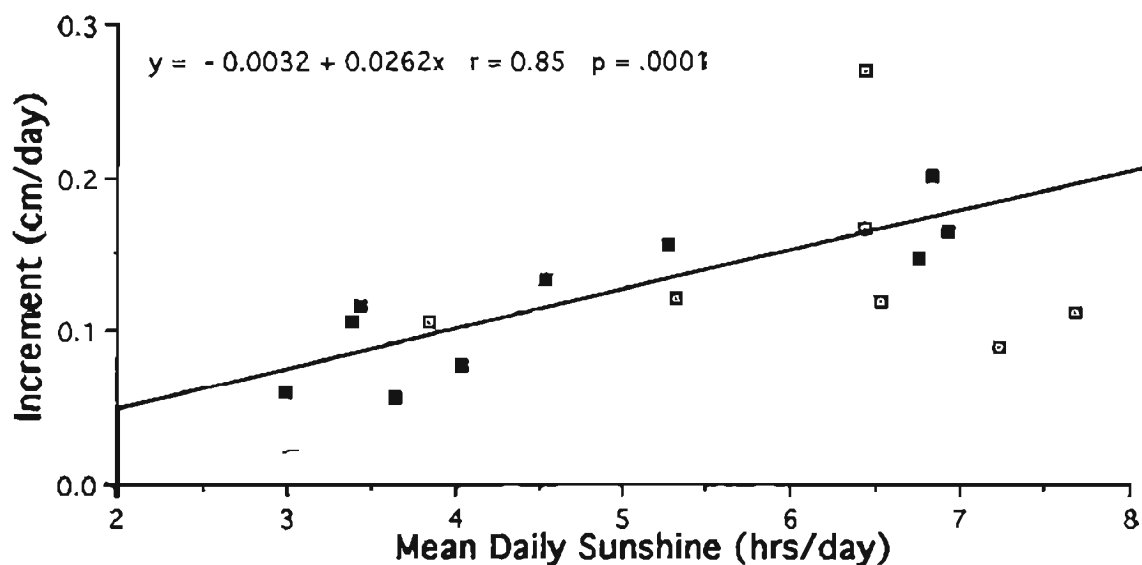


Fig. 6.9 Increase in length of *Phyllospora* branches against average daily sunshine. Points corresponding to temperatures averaging greater than 14.5°C (open points) have been deleted from the regression.

a) George III Reef.



b) Bicheno

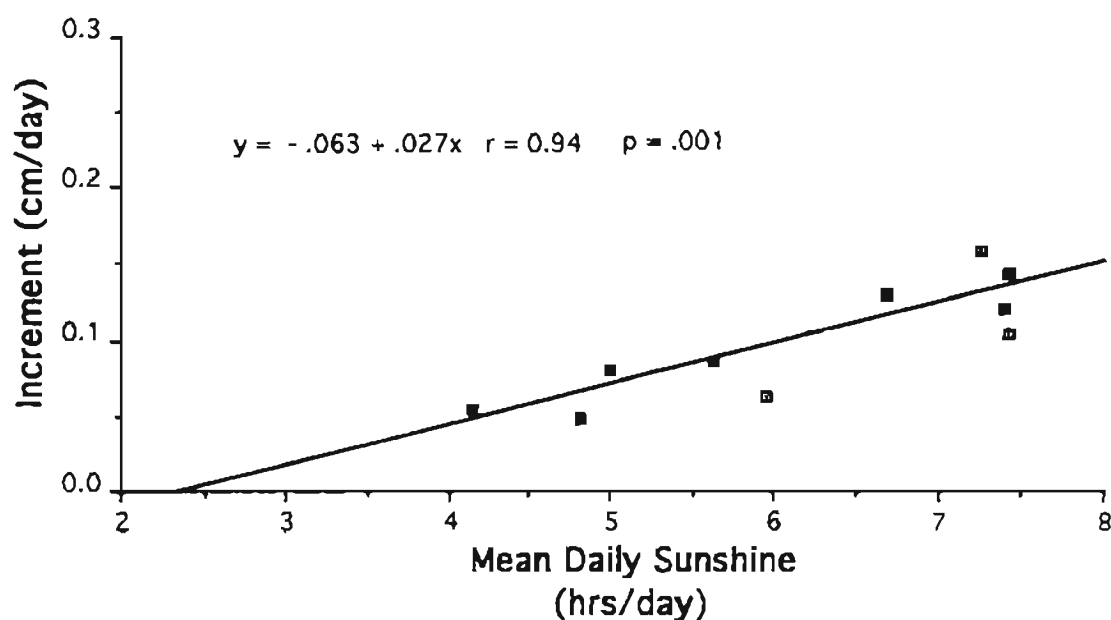
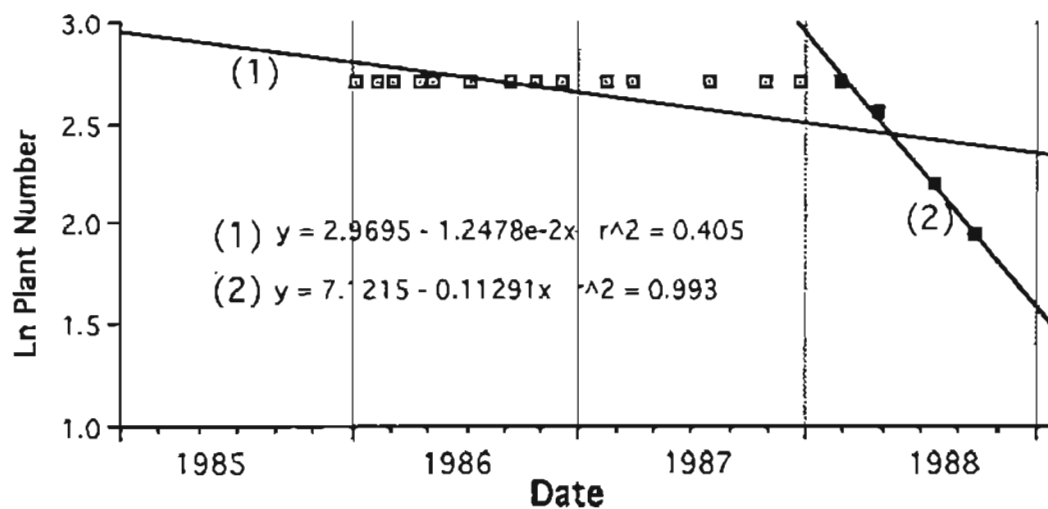
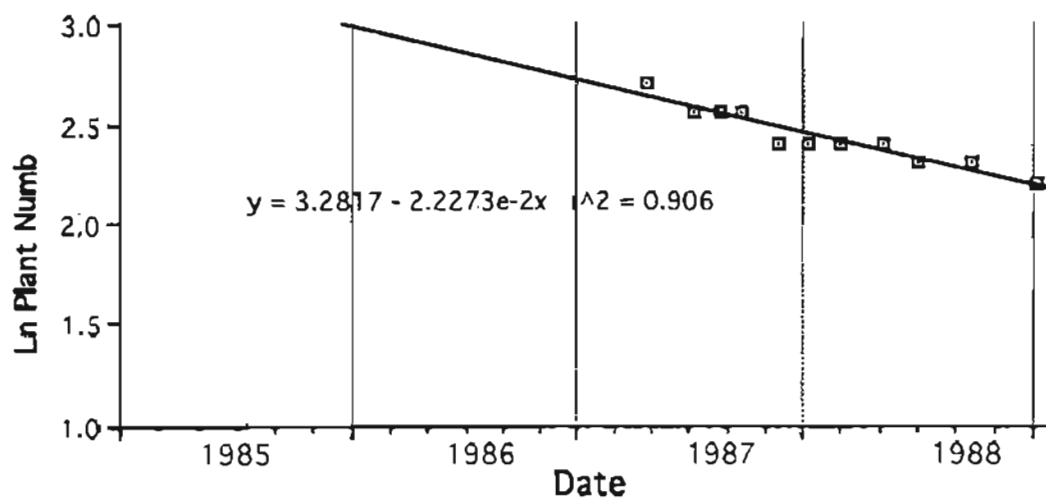


Fig. 6.10 Natural log. of number of original number of tagged plants versus time for both sites or 'depletion curves'.

a) George III Reef

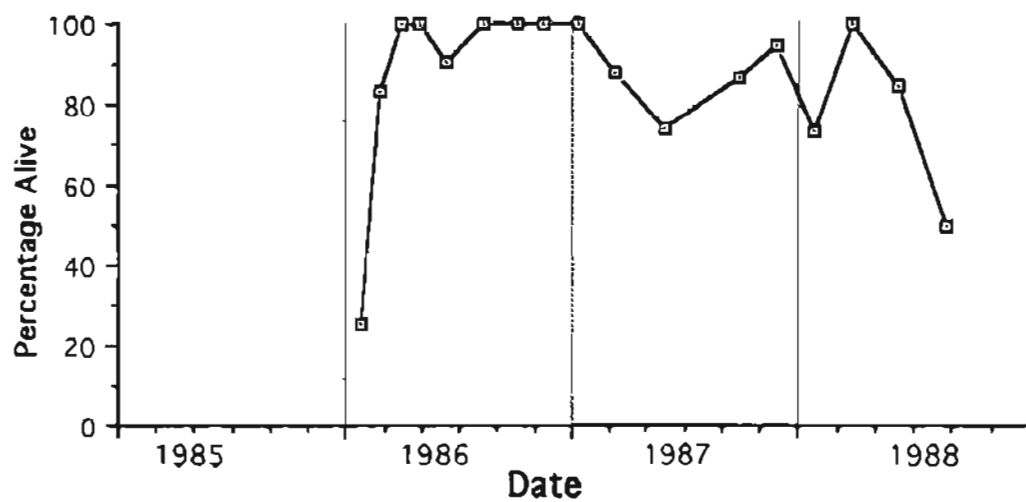


b) Bicheno.



**Fig. 6.11 Branch mortality. Percentage number living between sampling sessions.**

**a) George III Reef.**



**b) Bicheno.**

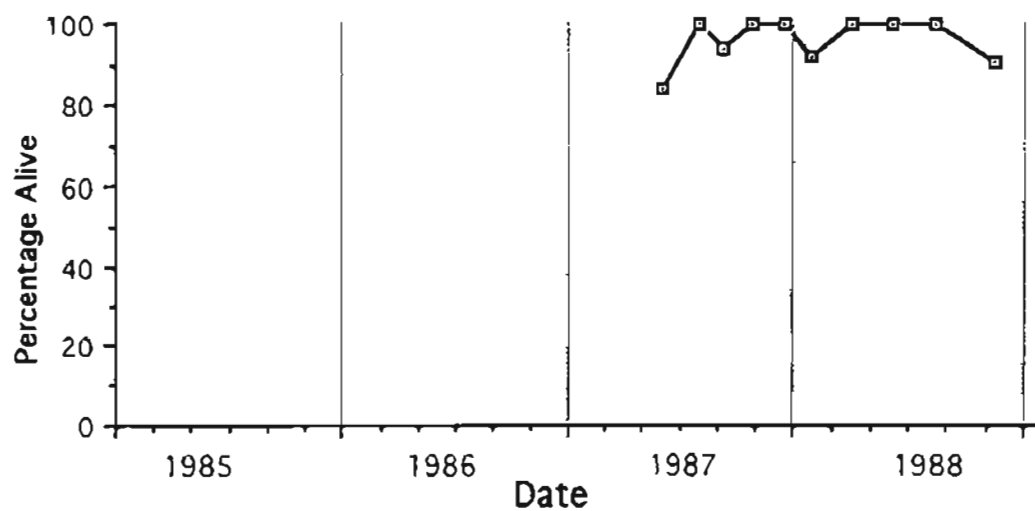
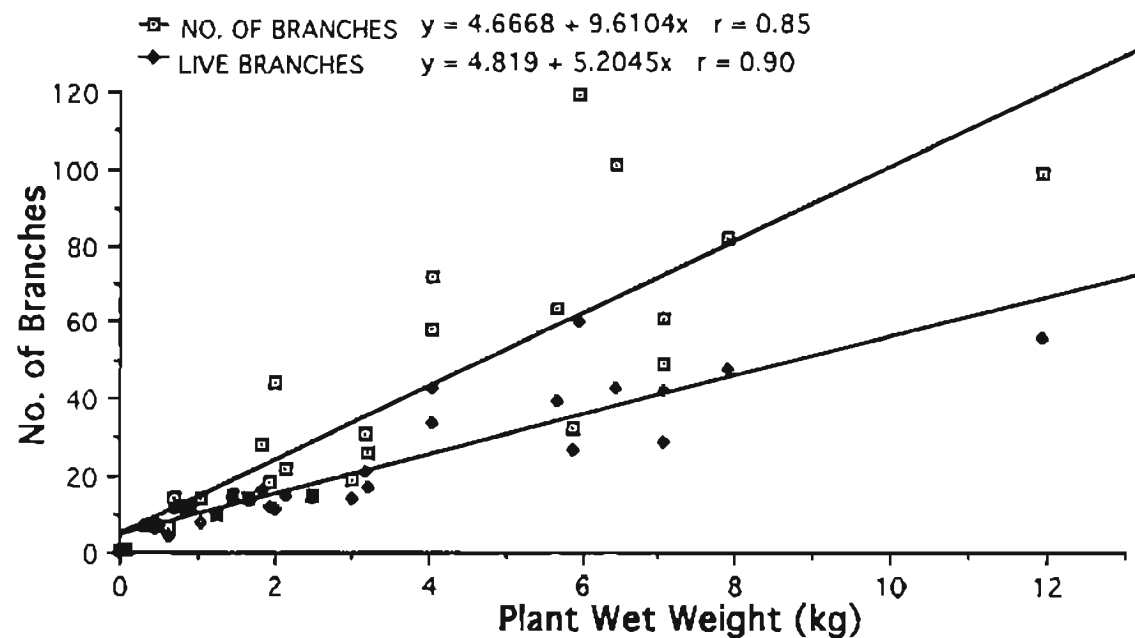
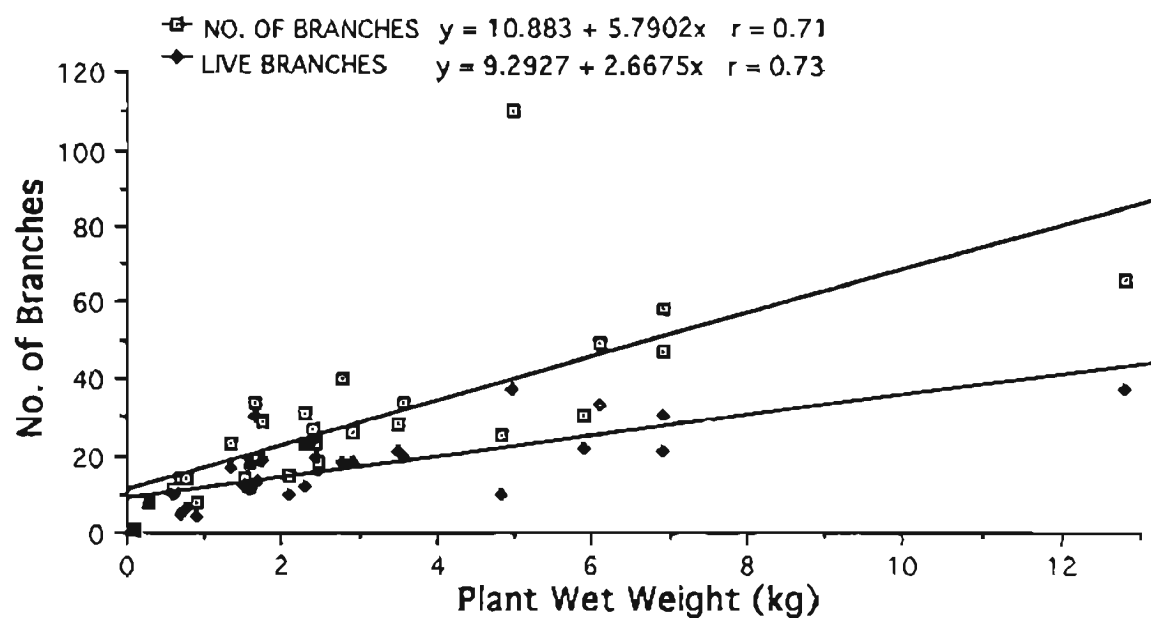


Fig. 6.12 Total number of branches and number of living branches per plant for a) summer and b) winter harvested plants at George III Reef.

a) Summer



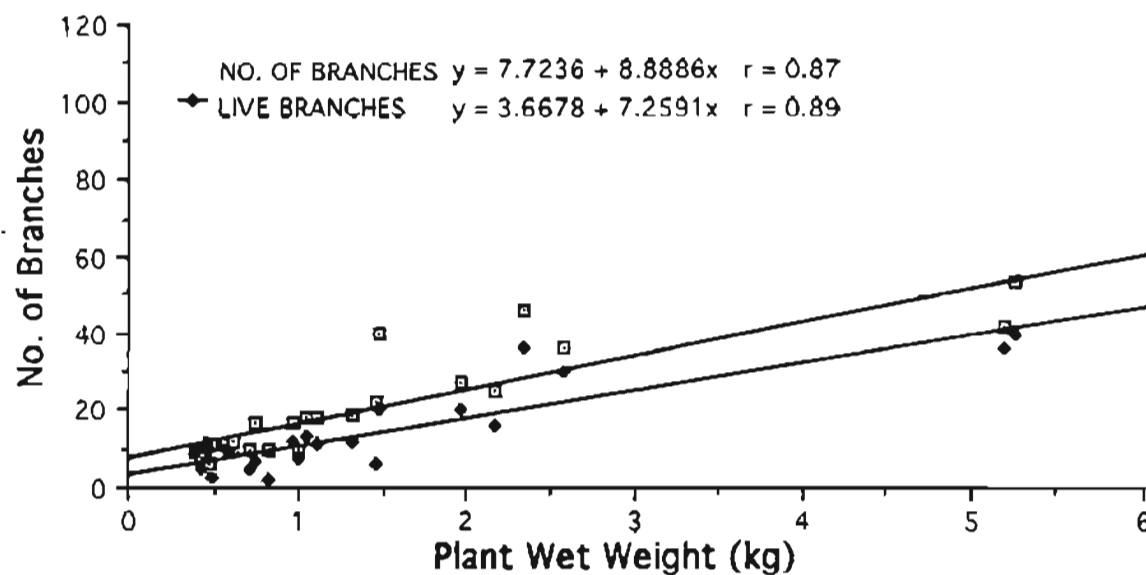
b) Winter





**Fig. 6.13** Total number of branches and number of living branches per plant for a) summer and b) winter harvested plants at Bicheno.

**a) Summer**



**b) Winter**

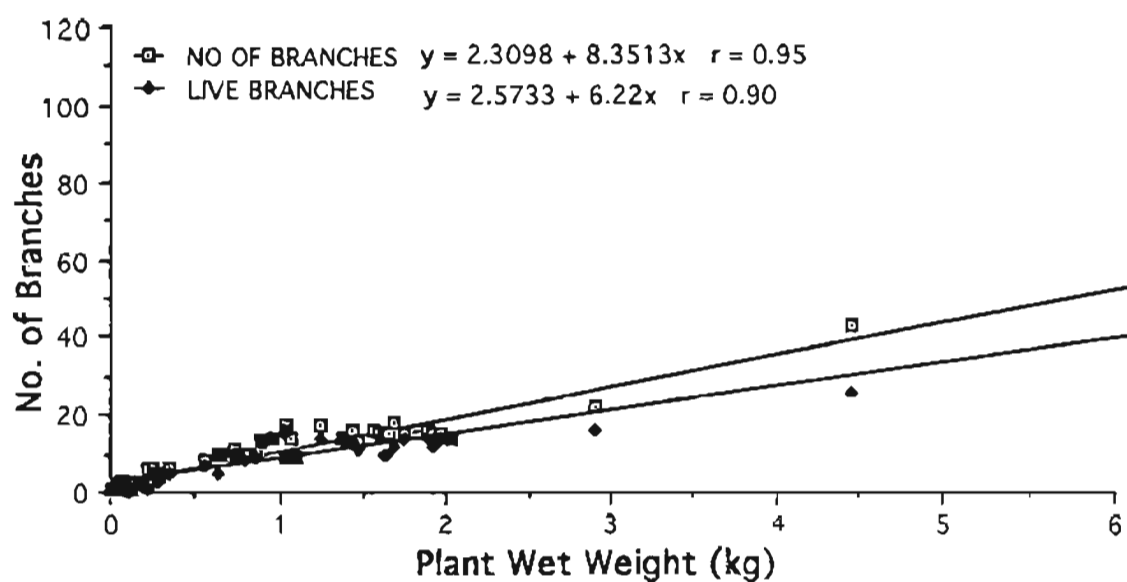
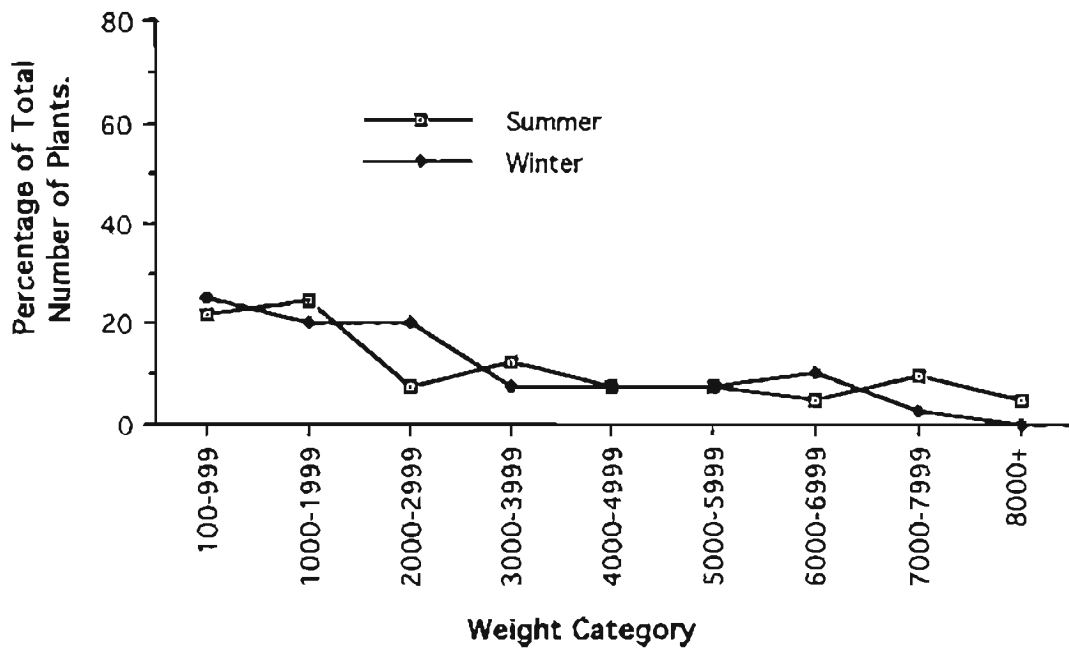


Fig. 6.14 Weight distribution of plants harvested.

a) George III Reef.



b) Bicheno

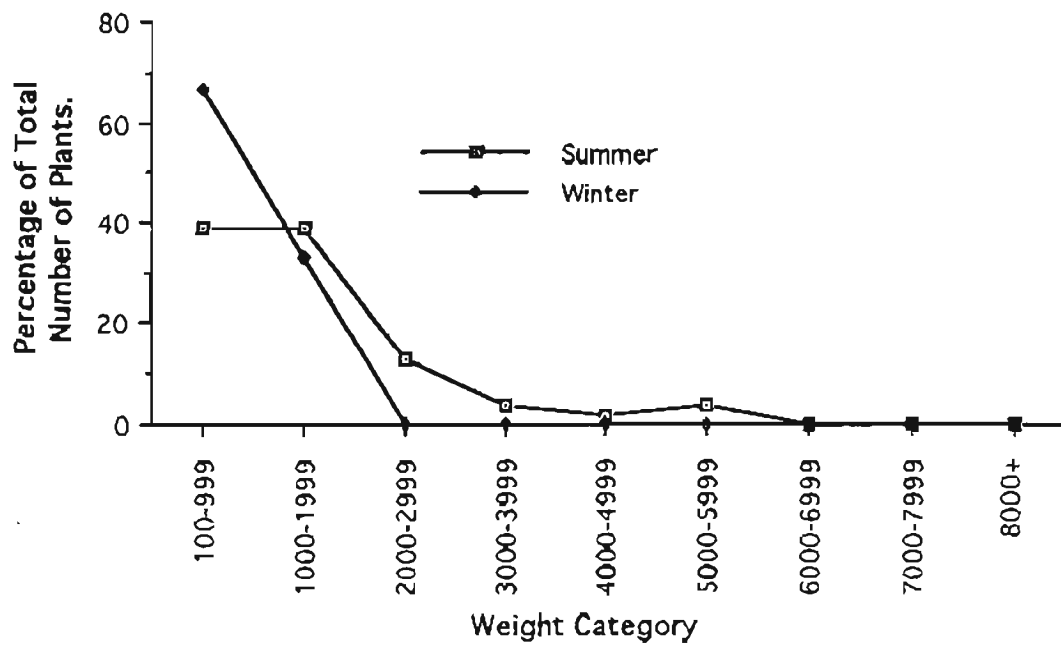
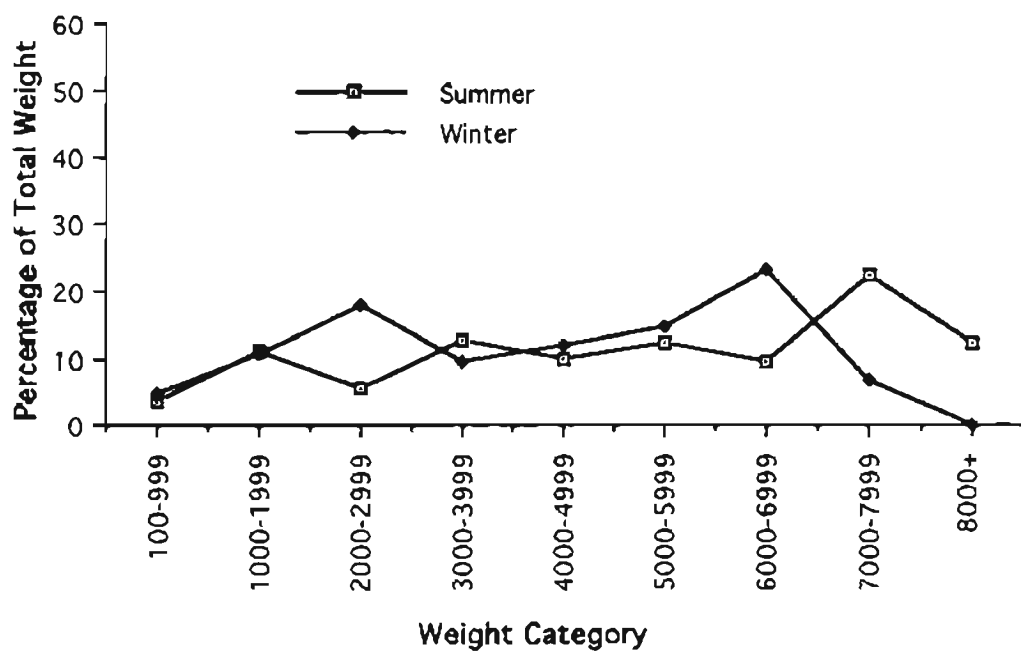


Fig. 6.15 Distribution of total weight between weight classes.

a) George III Reef.



gus.

b) Bicheno

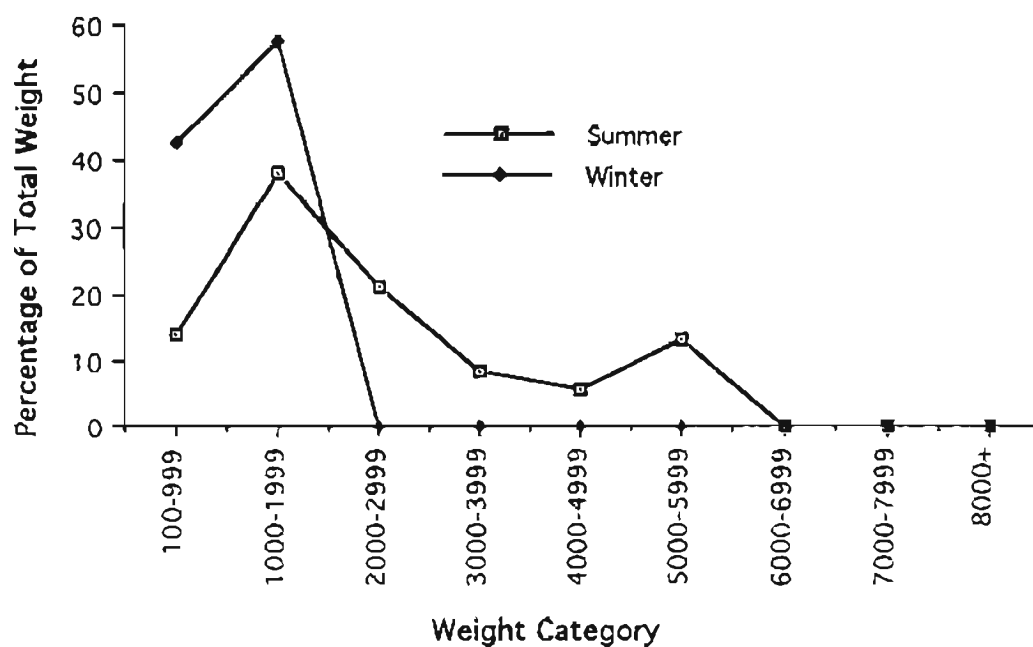
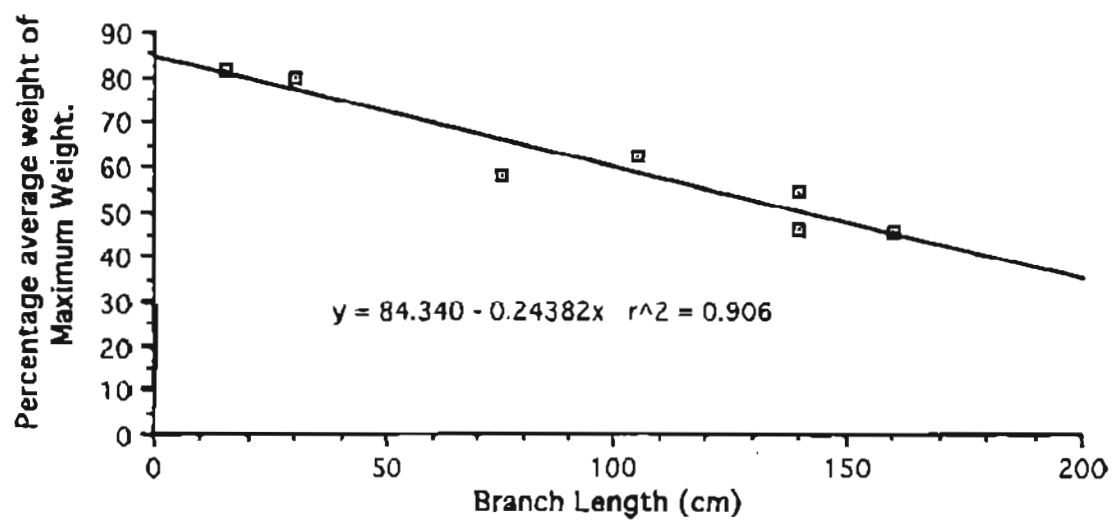


Fig. 6.16 Maximum weight per cm versus the total length of the lateral.



## PART 2, CHAPTER 7.

### THE RED ALGAL COMMUNITY AT GEORGE III REEF.

#### INTRODUCTION

The red algae are a very prominent part of the flora below 8 m at George III Reef. The effect is that of a red carpet. At the initiation of the study these algae were understory to a well-developed *Macrocystis* canopy. At the completion, the canopy had disappeared and aside from isolated plants of *Macrocystis*, *Ecklonia*, some other brown algal species and the seasonal appearance of patches of the green alga, *Caulerpa flexilis*, the red algae were the dominant plant group. It was because of this dominance and the likely input of the red algae into the overall biomass that it was decided to study this community. While the primary interest was change in biomass with time, species composition and change in sexual status of the more prevalent species was also determined as no subtidal work had been done on these communities in Tasmania. A similar long term study has been carried out on the red algal flora at a site off Cape Northumberland in western Victoria (Shepherd 1980) and some of the approach adopted here can be attributed to that project.

#### METHODS

##### Species-area relationships

Species-area relationships were determined by harvesting 4 m<sup>2</sup> using a metre square quadrat divided into 20 x 20 cm squares and a paint scraper and a suction sampler for collecting the algae. In total, 100 (20 x 20 cm)

squares were harvested. Values for individual squares could then be combined into quadrats of different sizes for analyses.

#### Species and biomass change with time

To determine change of species and biomass with time,  $5 \times 1 \text{ m}^2$  were harvested on a regular basis and analysed for content in the laboratory. Quadrat size was based on similar previous studies where  $0.25 \text{ m}^2$  had been used in comparable situations (Russell 1972 and Prentice and Kain 1976). The decision on size was made before the results of the species/area relationship had been completed. The larger size was used to ensure adequate sample size. Quadrats were haphazardly placed and harvested from flat, upwards-facing surfaces between holdfasts of *Macrocystis*, where present in 9-12 m of water adjacent to the 120-200 m section of the transect. The *Macrocystis* canopy disappeared in the second half of 1987. To determine the possible affect of the canopy on the biomass of red algae at George III Reef, quadrats were harvested outside as well as inside a small *Macrocystis* patch still remaining in December 1988.

The algae collected were placed in a 5 % solution of formalin in seawater until a convenient time for sorting. Each bag of algae was allowed to drain for a standard 20 minutes before being sorted into algal species. After sorting, these were placed into separate self-sealing plastic bags for weighing, determination of reproductive status and further identification where necessary. Where difficulties were experienced in identifying individual algae, samples were sent to recognized taxonomists for their opinions. Herbarium sheets have been made of all algae and are lodged at the Tasmanian State Herbarium.

Reproductive condition of plants of a number species was monitored by subsampling up to five mature plants from each of the quadrats. These were pooled for each sampling session.

### Permanent quadrats

To monitor in-situ variation of plant biomass with time, three 60 x 40 cm quadrats were marked out on the sea floor adjacent to the 120 m section of the transect line in 12 m of water. Again quadrat size was based on other similar studies (Shepherd 1980). On a regular basis, every 2-4 months, a 60 x 40 cm quadrat divided into 10 x 10 cm squares with 10 cm legs was placed over the areas and tracings done of the algae and heights measured. This part of the study was initiated in November, 1986.

Two diagonal corners of the quadrats were marked with household bricks. This proved not effective as one quadrat was unlocatable after 3 months. This was replaced by a second, but this too was moved by swell action. A second of the three initial quadrats disappeared after 18 months and only one remained until it was harvested in August 1988.

Mapping of the quadrats allowed individual plants to be monitored through time. Tracings were taken from original maps, cut out and weighed. Using weight/area regressions of the paper, changes in area with time of individual plants was monitored. Estimates of the change in biomass of the plants in the permanent quadrats were made with regressions of area or height to weight for specific species (see Appendix 5 for results) from algae from the harvested quadrats.

Identification of some of the species was not always certain underwater, especially where reproductive material was required. The thallus morphology of *Plocamium dilatatum*, for example, is very similar to *Plocamium costatum* and can only be distinguished on the basis of reproductive structures. *Plocamium costatum* is rare however and none was positively identified in this study. Where either *P.dilatatum* is specified or *P. dila.cost* then read "probably *P. dilatatum*". Similar problems were encountered with *Phacelocarpus* spp and *Peyssonnelia /Sonderopelta* spp.

### Statistics

Statistics used in this chapter are the same as those specified in Chapter 3 & 4. Analysis of variance (ANOVA, Sokal and Rohlf 1969) were performed on the data to determine the statistical significance of differences between means.

## RESULTS

### Species-area relationships

The concept of a minimal area for sampling is such that a minimal area must be sampled before the sample can be considered to be representative of the community. In Figure 7.1 the results of the 4 m<sup>2</sup> quadrat clearing are displayed (see Appendix 6 for full results). They show 28 species per 1 m<sup>2</sup> which is 68% of the total number harvested in 4 m<sup>2</sup> and 41% of the total of 69 species found in all harvested quadrats (44 m<sup>2</sup>). The 5 m<sup>2</sup> areas harvested each sampling session averaged 29 ( $\pm 1.4$ ) species. According to Grieg-Smith (1964) the validity of determining a minimum area depends on whether there exists some point where a marked decrease in the amount of information obtained. For practical purposes this is shown by the point at which the species-area curve begins to flatten out. Results show (Fig. 7.1) that the chosen sampling area (5 x 1m<sup>2</sup>) was well representative of the population and the quadrat size (1 m<sup>2</sup>) gives a good representation of the number of species. The quadrat size used, compares with 0.25 m<sup>2</sup> for both Russell (1972) and Prentice and Kain (1976) and various other sizes from 0.07 m<sup>2</sup> (Littler & Murray 1975) to >200 m<sup>2</sup> (John *et al.* 1977).

Much debate has occurred on the mathematical form of species-area curves (see reviews by Hopkins 1955, Preston 1962 and Dony 1977). As well as graphs of number of species to area on a linear scale, the various data sets have been plotted on a log species-log area scale and a species-log area scale.



The log species-log area method of Arrhenius (1921) tests the hypothesis that the number of species increases exponentially with increasing area and a species-log area scale, that of Gleason (1922) the hypothesis that there is a constant increase in number of species with increasing area. Both hypotheses have been applied to terrestrial vegetation over relatively small areas. For larger areas Dony (1977) found that there was a change in species-area relations in which the rate of increase changes from an exponential to a logarithmic one.

Log area and area against log number of species (Fig. 7.2) supports neither Arrhenius' or Gleason's hypotheses regarding species area relationships. This finding was also made by Dony (1977) for terrestrial vegetation for areas of intermediate size and Shepherd (1980) in a similar experiment on subtidal vegetation off Cape Northumberland, South Australia. Similar to the findings of Shepherd (1980) and Preston (1962, for many plant communities) a change in slope is interpretable (just, see Fig. 7.3) This interpretation is supported by extrapolation of the lower regression line indicating the mean area occupied by a plant as 11 cm<sup>2</sup>. Intuitively, this appears to approximate the average area of an individual plant.

#### Harvested quadrats

Full details of harvested quadrats are contained in Appendix 7. Analysis of variance on the data from the sets of quadrats harvested from inside and outside the *Macrocystis* forest at George III Reef showed a greater biomass for quadrats outside ( $p < .05$ ). Values outside the canopy were approximately double the values under the canopy.

ANOVA on change in species number on the sets of harvested quadrats in December 1988 (Fig. 7.4) shows no significant difference for presence and absence of the *Macrocystis* canopy for the two sets of quadrats harvested in December 1988.

### Factors affecting total biomass

Regression of biomass against average sunshine and sea-state combinations for one, two and three months prior to harvesting of the quadrats reveals sunshine for two months as giving the best regression ( $r = .81$ ,  $p = .015$ ). If it is assumed that the *Macrocystis* canopy decreased the light availability by 25% (see Chapter 2), and sunshine values are adjusted accordingly, ie. 25% less sunshine for the quadrats harvested when the canopy was present, then the regression is markedly improved ( $r = .89$ ,  $p = .0027$ , Fig. 7.17) and may be represented by the equation:

Quad Mass =  $393.7 + 363.9 \times \text{SUNSHG}$  (Over 2 months prior to sampling less 25% for periods where *Macrocystis* canopy present).

Of the species harvested from the quadrats, *Plocamium dilatatum* was three times more prevalent than the next species in terms of biomass. The incidence of the species in terms of the number of quadrats they occurred in and the quantities in biomass are presented in table 7.1 with results from Shepherd (1980) for comparison.

**TABLE 7.1** Ten most common species by biomass (g/m<sup>2</sup>) at George III Reef (10-12m depth) and at Cape Northumberland (10-15m depth, Shepherd 1980).

George III Reef		Cape Northumberland	
<i>Plocamium dilatatum</i>	1317	<i>Phacelocarpus</i> spp.	606
<i>Sondero. sp</i> / <i>Peyssonni. sp</i> *	211	<i>Plocamium dila./cost.</i>	341
<i>Plocamium angustum</i>	210	<i>Nizymenia australis</i>	291
<i>Callophyllis</i> spp.	116	<i>Hymenena affinis</i>	285
<i>Phacelocarpus</i> spp.	90	<i>Callophyllis lambertii</i>	214
<i>Caulerpa flexilis</i>	86	<i>Sondero. sp</i> / <i>Peyssonni. sp.</i>	138
<i>Thamnoclonium dichotomum</i>	44	<i>Ballia callitrichia</i>	88
<i>Ptilonia australasica</i>	31	<i>Myriogramme pristoidea</i>	86
<i>Plocamium mertensii</i>	19	<i>Rhodophyllis multipartita</i>	75
<i>Mastophora canaliculata</i>	17	<i>Melanthalia cochinia</i>	71

Ten most common species (likely incidence per 2 x 1 m<sup>2</sup> quadrat).

<i>Plocamium dilatatum</i>	1.00	<i>Plocamium dil./cost.</i>	1.00
<i>Plocamium angustum</i>	1.00	<i>Nizyenia australis</i>	1.00
<i>Sondero. sp / Peysson. sp</i>	0.97	<i>Hymenena affinis</i>	1.00
<i>Carpoveltis phyllophora</i>	0.95	<i>Ballia callitrichia</i>	1.00
<i>Ptilonia australasica</i>	0.93	<i>Myriogramme pristoidea</i>	1.00
<i>Rhodomenia australis</i>	0.90	<i>Rhodophyllis multipartita</i>	1.00
<i>Callophyllis spp.</i>	0.89	<i>Phacelocarpus spp.</i>	0.93
<i>Crassilingua marginifera</i>	0.88	<i>Callophyllis lambertii</i>	0.93
<i>Mastophora canaliculata</i>	0.84	<i>Sondero. sp / Peysson. sp</i>	0.93
<i>Plocamium mertensii</i>	0.84	<i>Melanthalia cocinnia</i>	0.93

\* Read *Sondero. sp / Peysson. sp* as either *Sonderopelta sp.* or *Peyssonnelia sp.*

Species present in the summer only include the leafy ephemerals, *Acrosorium uncinatum*, *Austrophyllus sp. (?)*, *Glaphrymenia pustulosa*, *Hemineura frondosa*, *Kallymenia cribosa* and the filamentous species, *Dasya sp.*, *Polysiphonia sp.* and *Ptilota hannafoordii*. *Caulerpa flexilis* was a major contributor to overall biomass but only on a seasonal basis. Some areas of reef bottom were covered with many kilograms of *Caulerpa flexilis* per m<sup>2</sup> in the summer but no erect axes were seen in the late summer - winter period; the rhizoids of this species over winters.

Before the disappearance of the *Macrocystis* canopy, *Phacelocarpus* spp. were present in much greater quantities than after and vice-versa for *Thamnoclonium dichotomum*. This could be as a response to changes brought about by the loss of the *Macrocystis* canopy, i.e. increased light and greater exposure to water motion due to the loss of the cushioning effect of the *Macrocystis* on wave action. Other species apparently affected by the loss of the canopy include an increase in relative amount of *Crassilingua marginifera* and a decrease in *Delisea fimbriata*.

#### Sexual status of red algal species

Reproductive status was monitored in a number of species but only two had a sufficient number of plants for confident analysis (*Plocamium*

*dilatatum*, *P. angustum*) and two were marginal (*P. mertensii* and *Ptilonia australasica*). The results are presented in Fig.7.7. *Plocamium dilatatum* is fertile from late summer to late spring. *Plocamium angustum* and *Plocamium mertensii* peak in fertility in winter. *Ptilonia australasica* peaks over the spring-summer period. These plants vary from predominantly tetrasporic for *Plocamium dilatatum* to predominantly sexual for *Ptilonia australasica*. Dominance of tetrasporic plants for *Plocamium* has also been demonstrated by Kain (1986) in the subtidal at the Isle Man.

#### Permanent quadrats

Overall change in biomass in permanent quadrats is presented in Figure 7.8. They demonstrate a decrease in total biomass over winter and an increase in biomass after the *Macrocystis* canopy disappears. Increase in biomass for the year November 1986-October 1987 was 113 % for quadrat 1 and 148 % for quadrat 2 for an average of 130 % (see Appendix 5). This would give production rates ranging from 2.5-4.5 kg/m<sup>2</sup>/yr from mean weight of harvested quadrats (Table 7.2). This compares with Shepherd's (1980) estimates of 4.5-5.4 kg/m<sup>2</sup>/yr at Cape Northumberland.

**TABLE 7.2** Estimated productivity of the red algal community at George III Reef assuming an annual turnover of 130 %.

Harvested quadrats	Av. Wt. (g/m <sup>2</sup> )	Est. Productivity. (g/m <sup>2</sup> )
All quadrats harvested	2319 ±128	3014
Quadrats under <i>Macrocystis</i>	1918 ±115	2493
Quadrats outside <i>Macrocystis</i>	3392 ±188	4409

## DISCUSSION

### Species area relationships

The total number of species found is less than that found by Shepherd (1980) in a similar study in South Australia. This however may be a reflection of differing phycological expertise and a more extensive sampling program. Many more of the smaller, less obvious algae were identified in Shepherd's study. Number of species/m<sup>2</sup> shows some similarity with the results of Shepherd however with approximately 40 species for a 4 m<sup>2</sup> sample and a flattening of the species-area graph between 1 & 2 m<sup>2</sup>.

There is a striking similarity in the actual species complement found at the two sites despite the distance (approx. 850 km.) and the physical barriers (Bass Strait and the west Tasmanian coast) separating the two areas. *Nizymenia australis* however is common at Cape Northumberland and undetected at George III Reef. *Melanthalia coccinea* is quite common at Cape Northumberland but only present in small numbers at George III Reef. Algae that are common at George III Reef but not recorded at Cape Northumberland are: *Caulerpa flexilis*, *Mastophora caniculata*, *Ptilonia australasica*, *Carpopeltis pylophora*, *Plocamium mertensii* and *Crassingula marginifera*.

### Growth Strategies

*Plocamium* spp., *Sonderopelta coriacea* and *Caulerpa flexilis* are the dominants in the red algal community and all three species have the capacity to spread vegetatively.

*Sonderopelta* is a flat 'platelike' alga attached by rhizoids. The platelike thalli of these plants increase and decay periodically. Shepherd (1980) estimated that plants can persist for up to three years, but the life history of individual 'fronds' was complete in about 6 months.

*Plocamium* spp. and in particular *P. dilatatum* are the most dominant plants in the red algal community at George III Reef. *Plocamium* spp. grow in two ways. First, the colony may expand laterally as the basal stolons spread over the rock surface, and secondly, individual fronds elongate by apical growth. Shepherd (1980) estimated that after attaining a height of 10(-15) cm after 2-3 months, they become reproductively mature, and finally slough off the rock at about six months. Evidence suggests that growth is not confined to peak growth times in the late spring-early summer, but *Plocamium* advances vegetatively to fill available patches in the community that may become available throughout the year. This is likely to give it a competitive advantage over algae such as *Ecklonia* in this area.

*Caulerpa flexilis* disappears completely in the autumn-spring period except for overgrown rhizoids. Early in spring, in areas not already dominated by *Plocamium dilatatum*, there is spectacular growth of *Caulerpa flexilis*. *Caulerpa flexilis* can be very abundant where the *Phyllospora* meets the red algal community in 8-9 m depth at George III Reef. Here, the action of swell can strip the rocks over the autumn-spring period, except for the rhizoids of *Caulerpa flexilis* and associated sediment and biota.

Dayton *et al.* (1984) suggests the more successful plants in kelp forests, subject to high wave stress, display similar characteristics of being short to prostrate and rhizomatous. This is consistent with these dominant plants at George III Reef.

Bicheno, at a comparable depth, has a relatively dense *Ecklonia* forest with an occasional *Macrocystis pyrifera* canopy. Why do the two sites display differing vegetational communities? Speculation as to possible reasons why the difference exists are; 1/ the wave climate and 2/ light availability

1/ Wave climate: While the average wave height at the two sites is similar, the types of waves are different. George III Reef is exposed to swell of a more consistent size, while Bicheno is subject to greatly disparate swell

sizes (see Chapter 2). The larger swells can be more destructive and regularly result in larger cleared patches. In this situation, *Ecklonia radiata* may be the more successful competitor. At George III Reef the conditions are more stable and large patches are rarely available. The red algal community, in gaining a solid footing, outcompetes the *Ecklonia*.

Light availability: Water clarity at George III Reef is poorer, and personal observation suggests that cutting of available light by overstory *Macrocystis* canopies in this area is of more regular occurrence than at Bicheno. Pearse and Hines (1979) demonstrated in a Californian kelp forest that the canopy of *Macrocystis* plants was limiting light penetration to levels below that necessary for the growth and survival of other brown algae and even the red algae. The light requirements for *Ecklonia* are higher than for the red algae as it is a mid-sublittoral alga (Lüning 1981; Chapter 2) so it is better suited to a higher light regime as is found at Bicheno. At Bicheno, red algae become more prevalent with depth (pers obs.).

Loss of the *Macrocystis* canopy may be compared to harvesting. The amount of light available to the subcanopy plants is increased and there is less protection from physical forces such as wave action. Some studies have examined the effect of *Macrocystis* canopy loss. Santileces and Ojeda (1984a) in a study off the Chilean coast, noted a loss in the second story *Lessonia flavicans* which was the most important understory producer. Its loss was unexpected as other studies in California had demonstrated an increase in lower strata cover. The loss may have been caused by bleaching effects of higher light intensity. Little difference in total biomass was recorded in the third stratum, equivalent to our red algal community, a group of fugitive species was replaced by a numerically similar group of fugitive species and the total number of species did not change significantly. Studies in California by, for example, North (1971) and Pearse and Hines (1979) have noted generally that with the loss of the *Macrocystis* canopy there is an

increase in the number of filamentous and foliose species and an increase in total biomass (up to seven times-North 1971). The findings in this study are largely consistent with these.

The apparent decrease in quantities of *Phacelocarpus* spp. and *Delisea fimbriata* and increase in the amounts of *Thamnoclonium dichotomum* and *Crassingula marginifera* may be due to differences in the physical constitution of the plants. The two former species are not as robust as the latter and their loss may be a response to higher water movement as a result of the disappearance of the *Macrocystis* canopy and the consequent loss of the buffering action from the swell. Red algal communities dominated by *Phacelocarpus* spp. (almost exclusively) can be found elsewhere in Tasmania on the east coast under thick *Ecklonia radiata* canopies in approximately 10-15+m of water (pers obs.). This suggests that *Phacelocarpus* spp. may be light or water motion sensitive. The study off Cape Northumberland (Shepherd 1980) found large quantities of *Phacelocarpus* spp., and this was in deeper water (approx. 14 m, thus relatively lower water movement) with a slightly higher mean value for the attenuation coefficient (0.206, n=13 and relatively lower light) than that determined for George III Reef supporting a water motion-light factor.

## SUMMARY

The presence of the *Macrocystis* canopy results in a halving of the red algal biomass/m<sup>2</sup>.

Some species appeared sensitive to the loss of the *Macrocystis* canopy. *Phacelocarpus* spp. and *Delisea fimbriata* were common before the canopy disappeared and *Thamnoclonium dichotomum* and *Crassingula marginifera* were more abundant after. This may be due to greater sensitivity of the former two to light and/or water motion and resilience on



the part of the latter. The second two species are both more robust in appearance in comparison to the former.

Of the algae monitored, peaks in 'reproduction' occurred in the period autumn-spring.

*Plocamium dilatatum* is 3 times more abundant than the next most prolific species.

Production of the red algal community under the *Macrocystis* at George III Reef is estimated at 2.5-4.5 kg/m<sup>2</sup>.

The three most abundant algae are rhizomatous and prostrate, this is believed to be an adaptation to high levels of water movement.

The species and the relative quantities found, show close affinity to a study done at Cape Northumberland, on Australia's southern coast, approximately 850 km to the north west.

The effect of the loss of the *Macrocystis pyrifera* canopy at George III Reef is similar to effects elsewhere after harvesting on the understory algal communities.

Fig. 7.1 Graph of number of species versus area of quadrat at George III Reef harvested on 26 May '85.

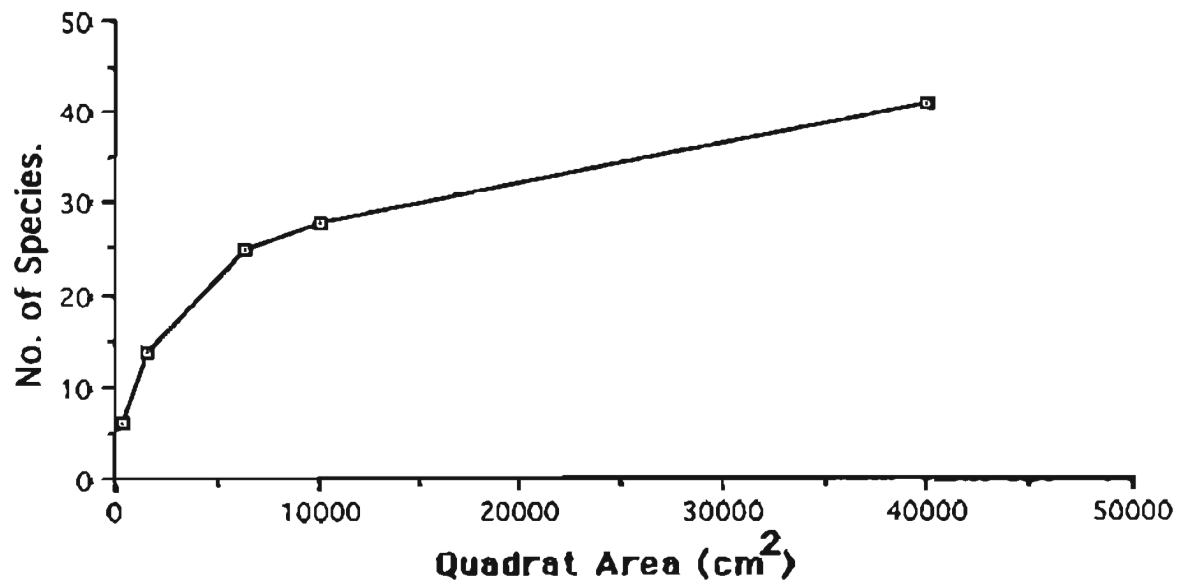


Fig. 7.2 Log number of species and number of species versus log area for George III Reef.

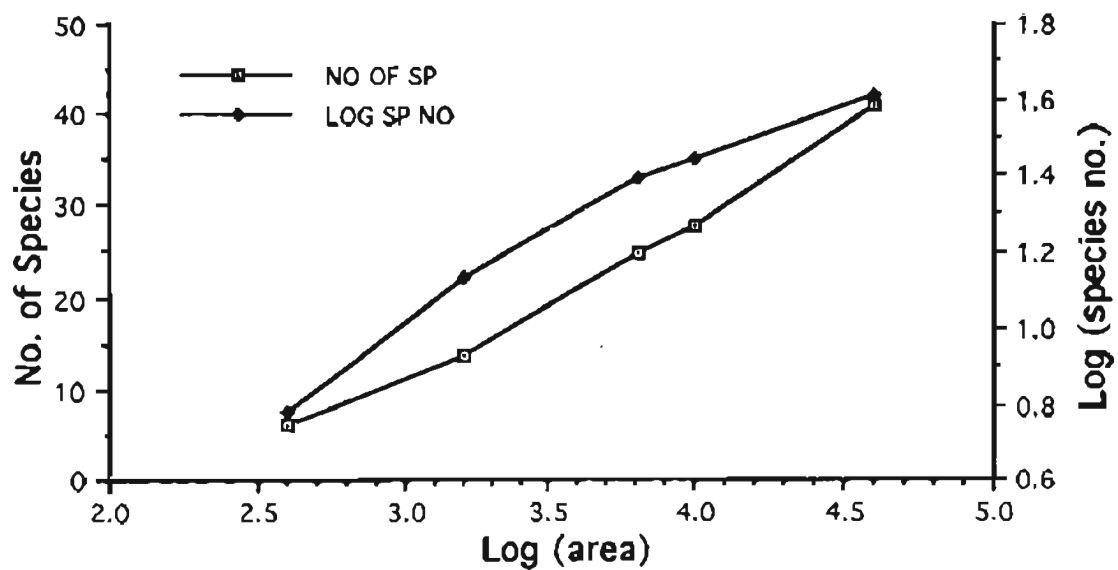


Fig. 7.3 Log number of species versus log area for George III Reef demonstrating the fit of two possible linear regressions.

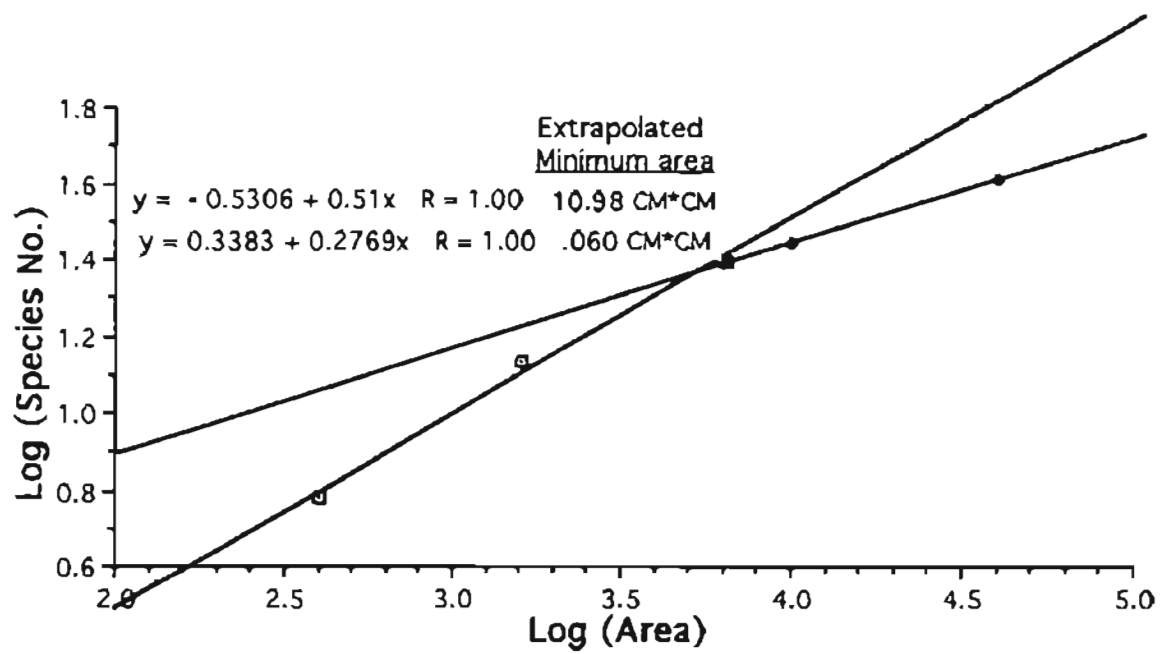


Fig. 7.4 Mean weight of all algae from harvested quadrats with standard errors.

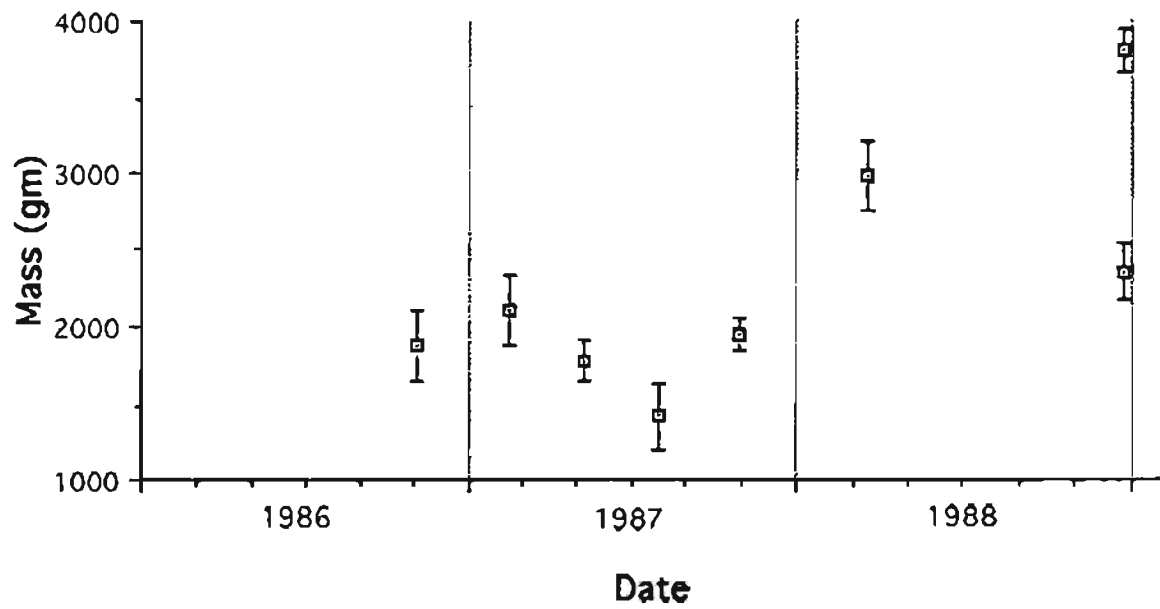


Fig. 7.5 Mean number of species in harvested quadrats with standard errors.

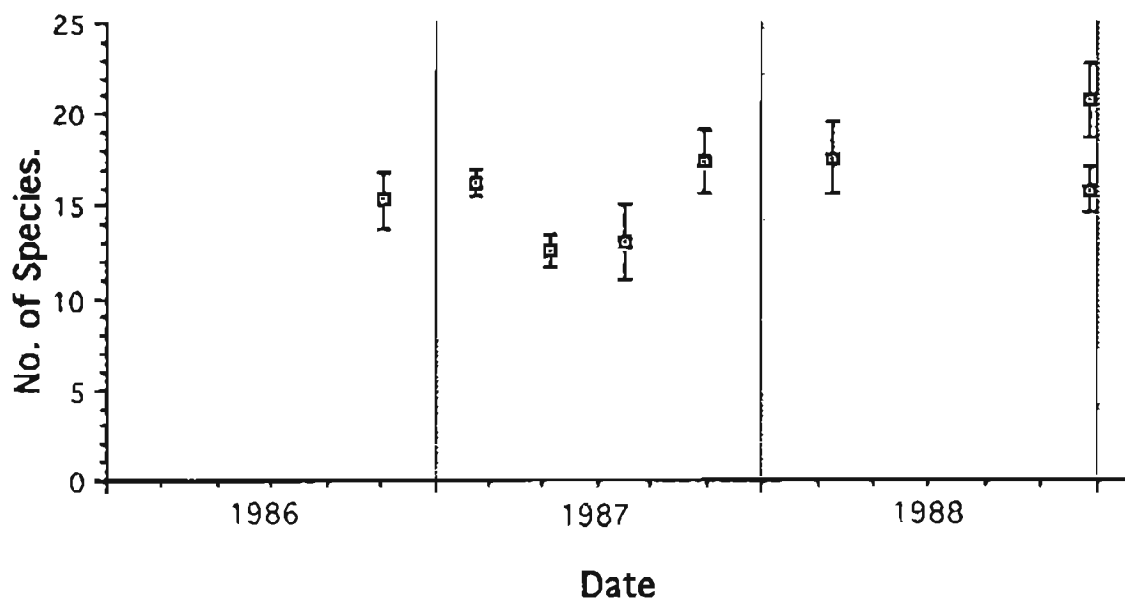
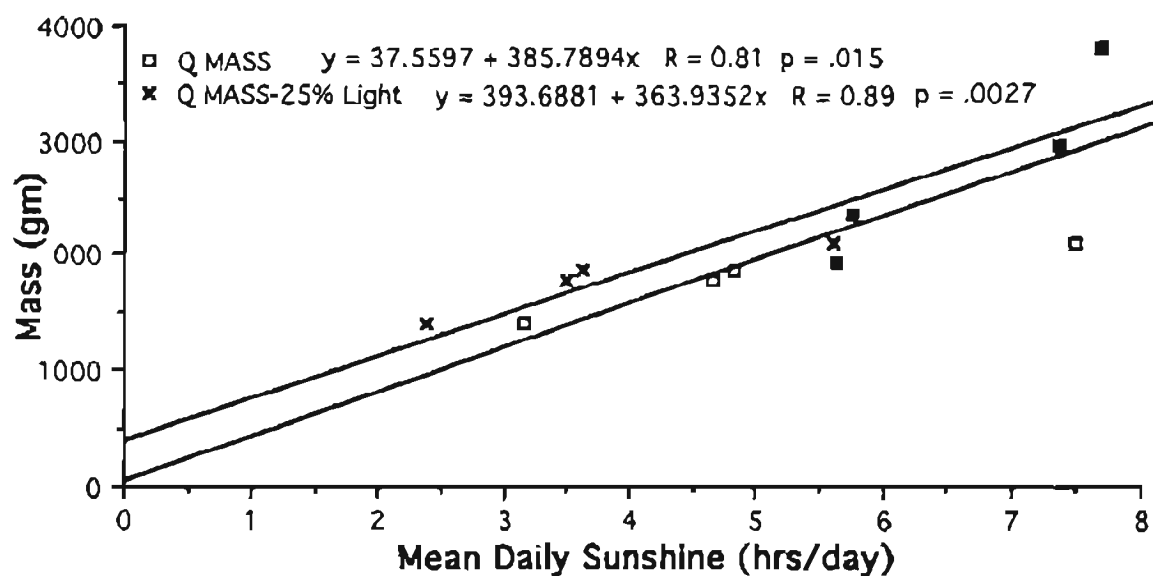


Fig. 7.9 Mass of quadrats against average sunshine for two months prior to harvesting. Regression is improved if light reduction of 25% due to *Macrocystis* canopy is accounted for in quadrats 3 Nov. '86 to 30 July '87 (filled squares are coincident points).



Figs 7.6 a to d show average total weight ( $\pm$ s.e.) of the major species in harvested quadrats. a) *Plocamium dilatatum* ( $\times 0.333$ ), *Sonderopelta coriacea*, *Plocamium angustum* and *Caulerpa flexilis*.

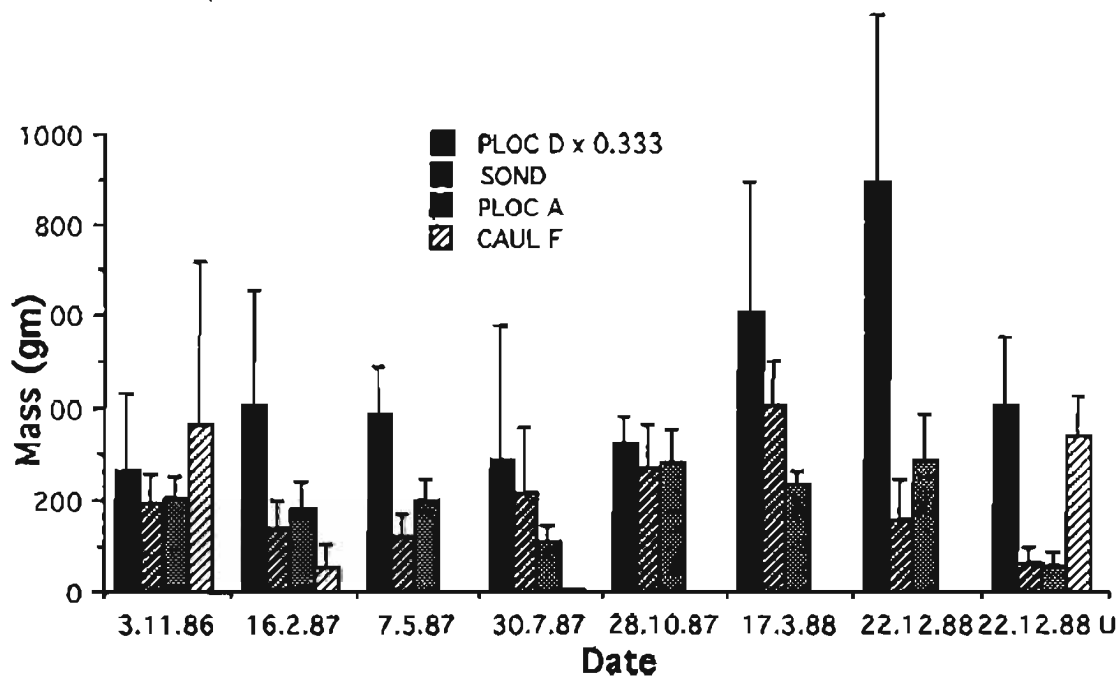
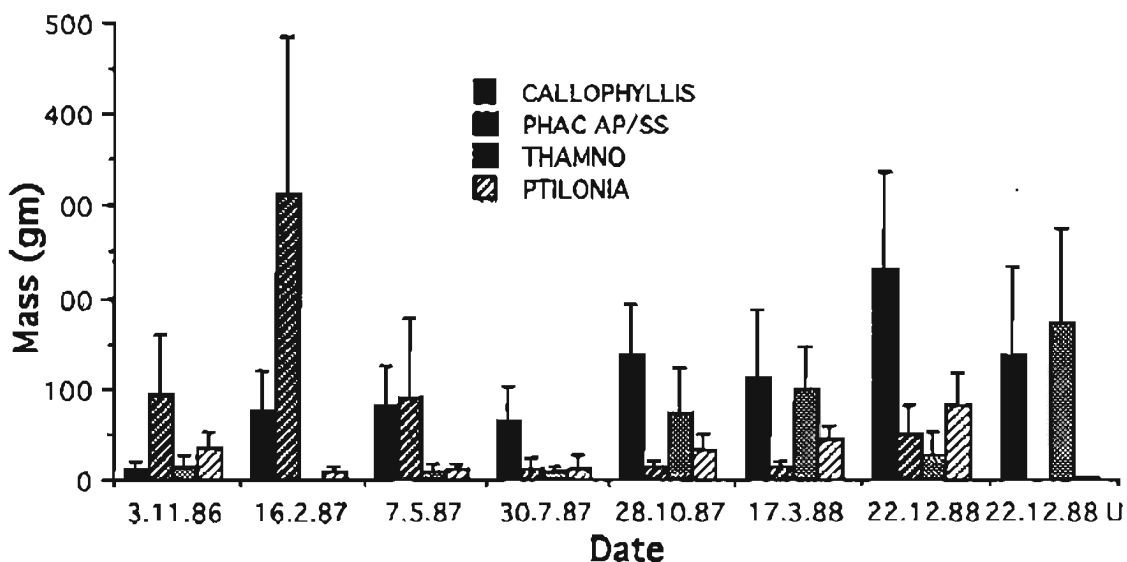
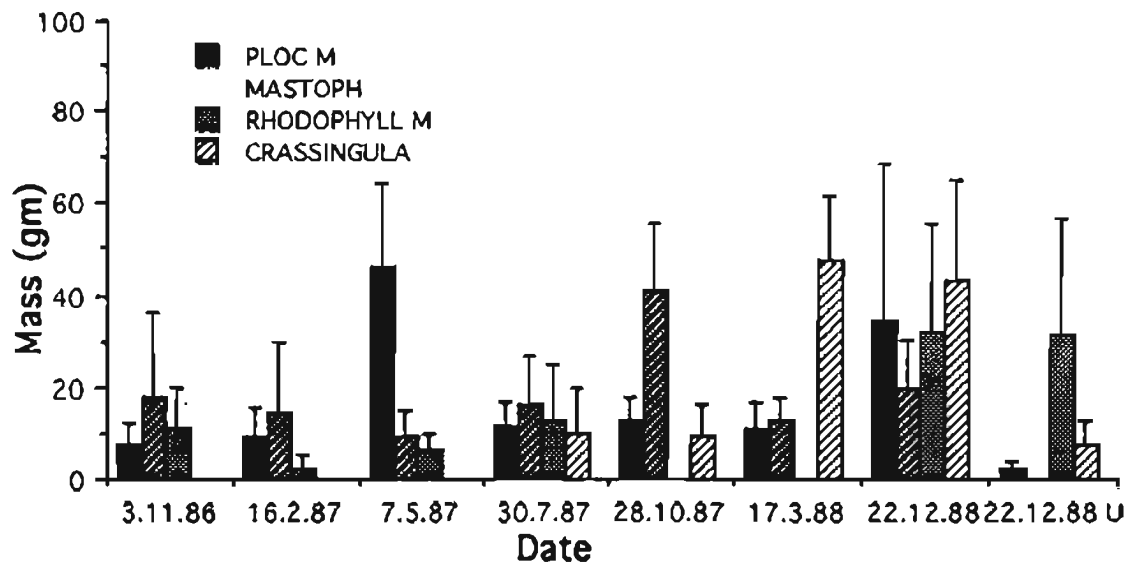


Fig. 7.6 b *Callophyllis* spp., *Phacelocarpus* spp., *Thamnoclonium dichotomum* and *Ptilonia australica*.



**Fig. 7.6 c** *Plocamium mertensii*, *Mastophora caniculata*, *Rhodophyllis multipartita* and *Crassingula marginifera*.



**Fig 7.6 d** *Carpopeltis phyllophora*, *Rhodymenia australis*, *Leptophyllis converferta* and *Hymenena* sp.

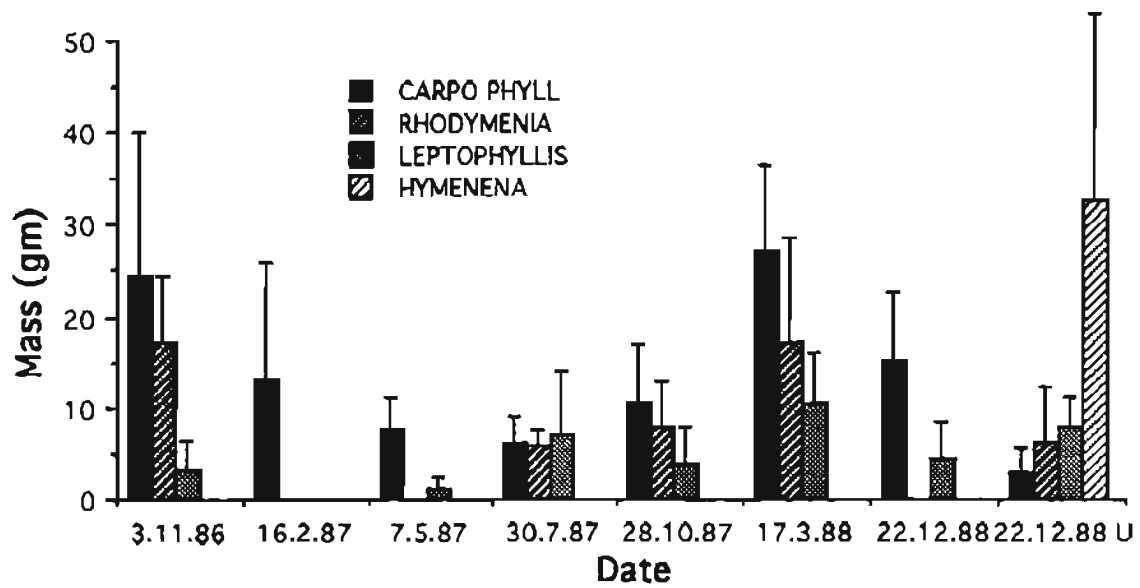
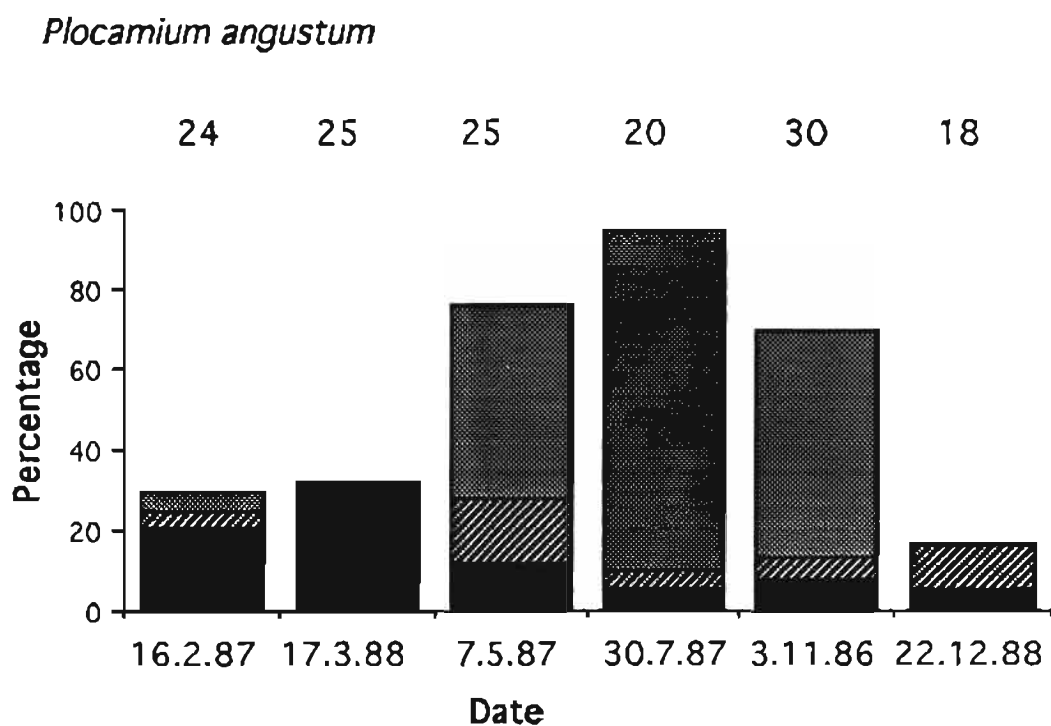
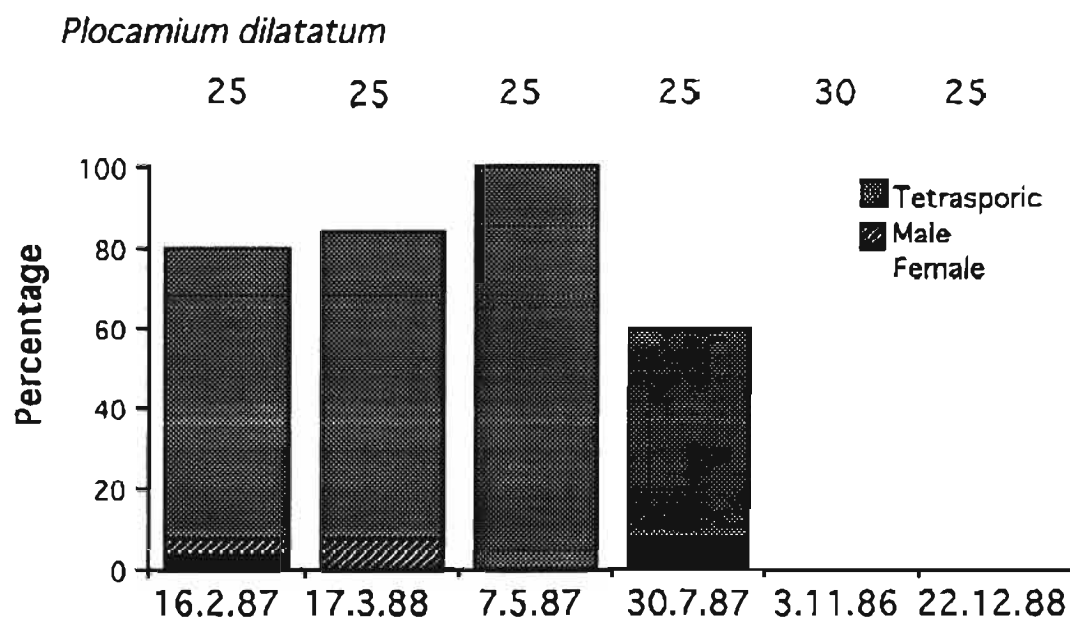
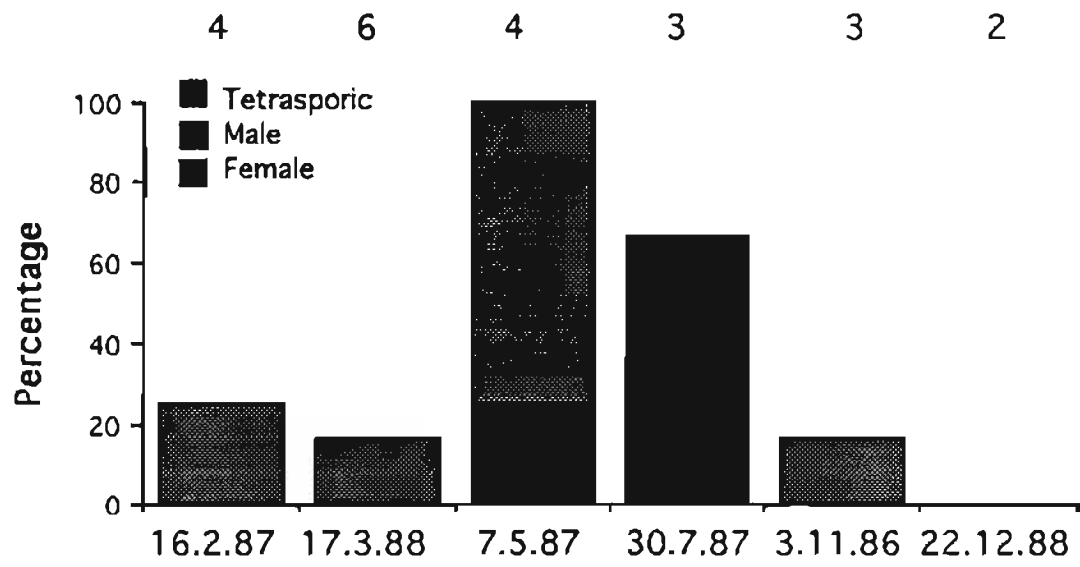


Fig. 7.7 detailing the sexual status of plants from harvested quadrats at George III Reef. Numbers at the top of the graphs are the number of plants used in the determination at each sampling period.





*Plocamium mertensii*



*Ptilonia australasica*

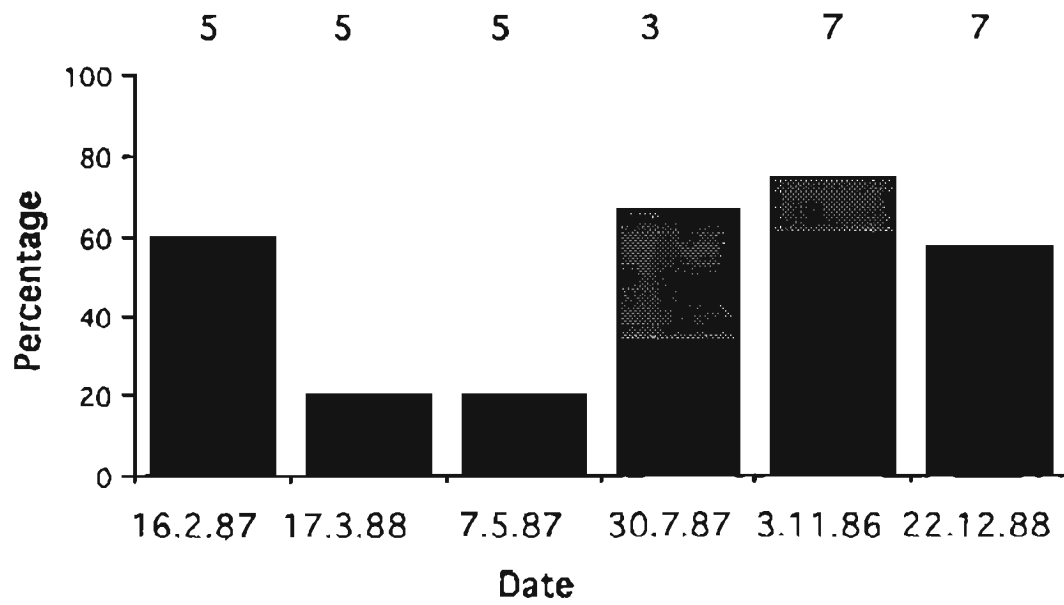


Fig. 7.8 a Calculated total weight of all species in permanent quadrat No. 1.

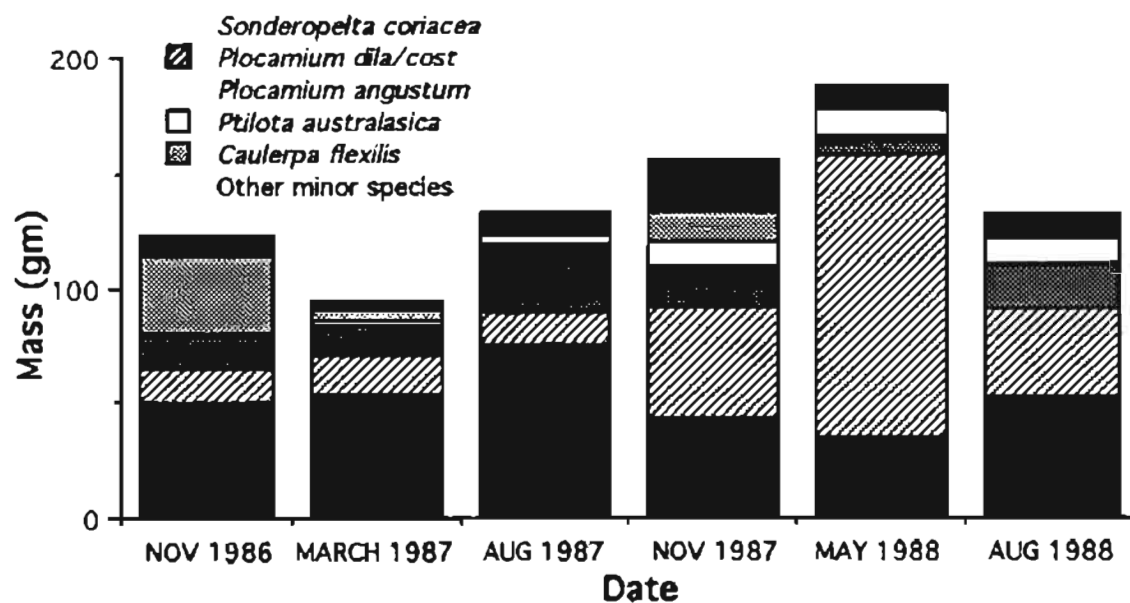
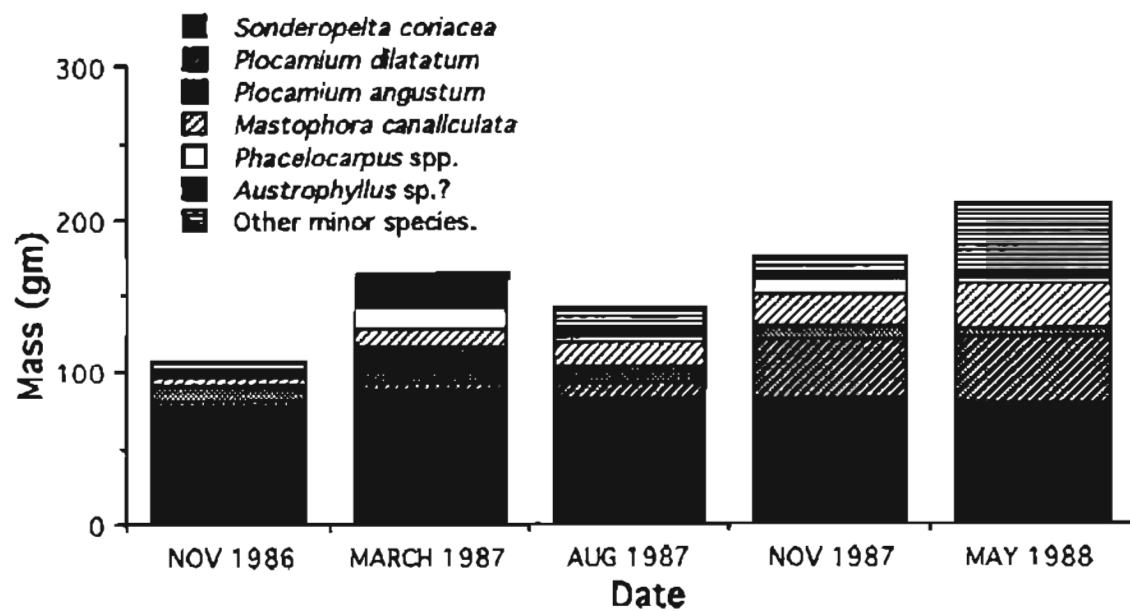


Fig. 7.8 b Calculated total weight of all species in permanent quadrat No. 2.



## PART 2, CHAPTER 8.

### MACROALGAL GROWTH IN COASTAL TASMANIAN WATERS

#### INTRODUCTION

This chapter ties in results of the previous chapters, and relates them to the principal aim. This was to investigate the seasonality, and major factors affecting the productivity of the dominant subtidal macroalgal species in Tasmanian coastal waters. Information thus acquired may aid in the interpretation of differing degrees of success in catching animal species in various parts of the state, especially of those animals dependent on macroalgae for food, such as the abalone *Haliotis rubra* Leach, and the sea urchin *Heliocidaris erythrogramma* Valenciennes. The following chapter attempts to relate these findings to observations on the abalone *Haliotis rubra*. The ultimate goal is to enhance our understanding of inshore coastal dynamics and thus improve the management of these fisheries.

In the chapter 'The Coastal Environment' the reasons for choosing the two sites Bicheno and George III Reef were given along with the results of the monitoring of physical parameters. These were compared with CSIRO results at nearby sites.

#### Macroalgal Communities

Both Bicheno and George III Reef were found to have communities with upper strata dominated by either *Durvillaea potatorum*, *Phyllospora comosa*, *Ecklonia radiata* or a combination of these species. *Macrocystis pyrifera* can also be dominant at both sites from 6-13 m depth, but its occurrence is intermittent. At George III Reef there is also a prominent red

algal community below 8 m depth. These dominant algal groups were chosen for more intensive study (the study of *Durvillaea* was later discontinued) the results of which are in preceding chapters. Principal factors affecting growth were determined for possible later extrapolation to other areas.

### Hydrographic Conditions

Differences in nutrient regimes between the two sites, contrary to expectation, were minimal, at least for the period monitored, the primary differences being water temperature and salinity. The Bicheno site was approximately 1°C warmer, with a mean salinity of 35.35 g/l compared to 34.98 g/l at George III Reef for a similar period. These results concur with CSIRO data from monitored sites in nearby areas.

The major factor affecting the oceanographic conditions around the state seasonally and on a year to year basis are the westerly winds. Differences between summer and winter can be attributed to the more northerly position of the high-pressure areas in the winter, allowing westerly winds to sweep across the Great Australian Bight driving subantarctic waters, and thus the subtropical convergence, up the east coast. How far this convergence extends northwards in the winter and southwards in the summer varies from year to year depending on pressure differences between the equatorial and temperate regions (Wyrski 1960).

Annual differences over the period of the study thus relate largely to interannual differences in the westerly wind stress. The summer of 1986-7 was a particularly windy summer and this is reflected in higher nutrient concentrations in the Storm Bay. The increase in the subtropical influence in the period 1987-1989 was coincident with a reduction in the westerly wind stress. Intrusions of subtropical water were detected by increased salinities and very low dissolved inorganic phosphorus (Harris *et al.* 1991).

The monitoring program at Maria Island was established by the CSIRO in 1946. Data from this station has demonstrated an increase in summer maximum water temperatures of at least 1°C over the period since inception, coincident with an increasing influence of the East Australian Current (EAC) down the east coast of Tasmania (Harris *et al.* 1987).

### Sea State

A comparison of the sea state of the east coast in the vicinity of Bicheno with the likely scenario at George III Reef shows that whereas it was assumed that exposure to wave action would be comparable, the Bicheno site was found to be open to more variable swells of a potentially destructive nature, further exacerbated by the aspect of the site.

### Potential Factors Affecting Macroalgal Growth in Tasmania.

The equations below (table 8.1), summarize the relationships determined between measured environmental parameters and growth of the algae. Basically, sunshine is the foremost factor affecting the growth of the algae. This is not really surprising as it is a plant's most basic requirement. This then implicates to a lesser degree factors that affect light attenuation such as the depth of the water, turbidity and sea state which all vary on a local basis.

The next most important factors are temperature and the availability of nutrients, primarily nitrogen, of which the interpretation of effect from the data is difficult due to its close relationship to temperature.

Temperature and nutrient availability are in turn affected by prevailing weather patterns and on a more local basis by water flow and the history of the sea-water. For example, water flowing south to north up the D'Entrecasteaux Channel (a shallow, sheltered water-course, mostly less than 20m deep, between Bruny Is and Tasmania), may be nutrient-enriched

at the southern end but nutrient-depleted at the northern. Bass Strait, also, is a relatively shallow (<200m deep) region, between Tasmania and mainland Australia. Water here does not benefit as readily from cooler nutrient enriched incursions found in deeper areas. The sea-water also tends to be confined between the eastern and western boundaries of the Bass Strait Islands and as a result the water here is warmer and relatively nutrient-depleted.

**Table 8.1** Summary of primary factors affecting the growth of the algae, from regression analyses as determined at the two sites.

Site & Plant	Growth index	Influencing Factors	Significance	Influence (+/-)	Half Life (months)
<u>George III Reef</u>					
<i>Ecklonia radiata</i>	Lamina increment	SUNSHG,	.0001	+	23
		TEMP20	.0002	-	
		& AVSWELL*	.0089		
	Erosion rate	NIT10	.0001	-	
		or TEMP20*	.001	+	
<i>Macrocystis pyrifera</i>	Blades/ 1st metre	SUNSHG	.0034	+	
		& TEMP20*	.03	-	
	Blade Increment	TEMP20 & NIT2WK*	.0001 .002		
<i>Phyllospora comosa</i>	Lateral Increment	SUNSHG	.0007	+	34.1
<u>Bicheno</u>					
<i>Ecklonia radiata</i>	Lamina increment	SUNSHB	.0014	+	10.4
<i>Phyllospora comosa</i>	Lateral Increment	SUNSHB	.0016	-	26.4

\* Cutoff significance levels of factors determined from stepwise regression were calculated taking into account candidate predictors as per Wilkinson and Dallal (1981).

Increased water temperatures in 1988 coincided with

1/. reduced growth rates in the Bicheno *Ecklonia* plants,

- 2/. the disappearance of *Macrocystis* at both sites and
- 3/. decreased growth rates, increased incidence of dying branch tips and plant loss of *Phyllospora* at George III Reef.

Factors are thus apparently affecting the algae over seasonal differences ie. from year to year. Harris et al. (1991) has associated the warm year of 1988 to the 'La Nina' phenomenon in which changes in oceanic circulation patterns affect climate and fisheries around the Pacific rim.

Other variables were apparently acting on the algae at levels other than the growth rates. Mortalities for *Ecklonia* and *Phyllospora* at Bicheno were at least half again as great as the George III Reef values over the study period. This is most likely attributed to the more variable wave action at Bicheno and/or warmer water.

Swell action and sea-state can have an over-riding effect on the nature of the community. At Bicheno, while individual algae were more productive, on an area basis, overall productivity of the macroalgae was less than potential. Much of the substrate at Bicheno was often bare due to the destructive nature of the swells and the scouring action of sand on the reef. More protected areas in the near vicinity of the site investigated had dense macroalgal cover from the low tide level down to the limit of substrate at 20+m.

The presence of macroalgae can have a modifying effect on the impact of swell. At Bicheno, more sand was noted on the reef after the disappearance of the *Macrocystis* and the *Ecklonia* seemed to be in poor condition. A drop in total length of the plants was observed over the period of investigation over and above any seasonal differences. This is thought to be due to the exposure of the area to the full force of the swell after the disappearance of the protective *Macrocystis* forest.

The maintenance of the composition of the macroalgal communities at the two sites investigated has many parallels with the investigations into

the kelp forests off the Californian coast. Dayton *et al.* (1984) noted that while *Macrocystis* was the most conspicuous and functionally-important species, it is one of the first species to be eliminated in physically (wave or sand scour)-stressed and grazer-stressed habitats. Resilience or recoverability was strongly dependent on oceanographic factors such as temperature, nutrients and water visibility, all of which are strongly influenced by longshore currents, by cross shore transfer via internal waves, by local weather conditions, and even by large scale climatological events that have a strong effect on the biota. Effects on all these scales are all evident in the Tasmanian populations of *Macrocystis*.

#### Transplants

Transplant experiments showed that for *Ecklonia* at least, morphology and growth strategies are partially genetically and environmentally determined. Lateral density and stipe length appeared to have a genetic component while plant length was environmentally decided. Adapted genetic traits are largely environmentally forced and in this case, may be related to high temperatures, low nutrients and wave action.

#### Coastal Production

From a representative transect on the adjacent coastline (Sanderson unpubl. Hons Thesis 1984), assuming similar biomass/m<sup>2</sup> levels, we can determine a productivity value for a typical metre of coastline in this area (see table 8.2). In table 8.3 likely relative contributions of each of the major species to overall biomass is calculated for the system at George III Reef.

Note the large contribution of *Macrocystis* to overall biomass. The loss of *Macrocystis* from much of the Tasmanian coast in recent years (Sanderson 1987 a) has greatly reduced the amount of biomass available to the coastal system. This becomes available through plant loss, loss of parts of



plants which are either eaten or degraded, erosion and dissolution as organic solutes and the action of herbivores. Perhaps more research should be invested in the reasons why this plant has disappeared and ways in which it can be returned.

**Table 8.2** Estimated annual production per metre of coastline.

Community	Depth Range (m)	Area (m <sup>2</sup> )	Standing Stock kg/m	Annual P/B ratio	Total Annual Production (kg)	% Total
<i>Durvillaea</i>	0-7	60	35+*	1 (?)	2100	60
<i>Phyllospora</i>	7-10	30	5.3	1.1	175	5
Red algal	10-14	50	4	1.3	260	7
<i>Macrocystis</i>	12-14	30	6.4	4	768	22**
<i>Ecklonia</i>	14-18	60	2.1	1.5	189	5
					<u>3492</u>	

\* From three random quadrats harvested at George III Reef see Appendix 8.

\*\* Note the small amount of coastline occupied by *Macrocystis* yet the high proportion of the total production.

**Table 8.3** Estimated annual production of macroalgae on George III Reef.

Community	Est. Area (m <sup>2</sup> )	Depth Range (m)	Standing Stock kg/m	Annual P/B ratio	Total Annual Production (tonnes)	% Total
<i>Durvillaea</i>	30,000	0-6	35	1 (?)	1050	46
<i>Phyllospora</i>	7,000	6-8	5.3	1.1	41	2
Red algal	70,000	8-13+	4.0	1.3	364	16
<i>Macrocystis</i>	15,000	8-18	6.0	4	360	16
<i>Ecklonia</i>	170,000	13-18	1.75	1.5	446	20
					<u>Total</u>	<u>2261</u>

### Herbivores

Much emphasis is placed on the effects of grazers, in particular sea-urchins, in north American studies. While sea-urchins are evident in Tasmania, they are rarely seen out actively foraging during the day, and it is doubtful if their presence is a significant determinant on community

processes at least in wave exposed areas. It is interesting to note that the significance of urchins in general is small in the southern hemisphere. Mann (1982), reported that the effect of urchins is limited in the New Zealand and Australian kelp beds and Dayton (1985) claimed urchin barrens are not common in South America. Grazing by molluscs such as the 'turban shell' or 'periwinkle', *Turbo undulata* (Lightfoot, 1786), the 'seaweed shell', *Phasionotrochus eximius* (Perry, 1811) and the 'abalone' *Haliotis rubra* may be more significant but not directly on the adult sporophyte stage of algae but through grazing of the microscopic gametophyte and juvenile sporophytes from the rock surfaces.

### Comments

Results of this study serve as a pilot for further work. Affects of nutrient limitation may be more properly assessed by comparing a northern Tasmanian coastal site with a southern. Comparison of an eastern site with a southern has more meaning in a year when there is a more distinct difference between the nutrient regimes. This is more likely to occur in years when the EAC does not venture further south than Maria Is.

To make results more meaningful in the terms of a study such as is required for a PhD, examination of a single species would be more appropriate. At sites such as Bicheno where there is apparently a large amount of local variation in physical and biological conditions, more intensive sampling is required to properly distinguish the variation within the area from variation between contrasting sites. More than two sites is required also to separate larger scale local variations from large scale oceanographic if this is to be the intention. Monitored plants for example, should be depth stratified to separate the effect of depth on growth rates at each site. In this manner the problem of pseudoreplication (Underwood 1981, Hulbert 1984) is more properly addressed. While this study has given

some interesting correlations these are not effects. More studies need to be done to prove them as causative.

Production estimates have been shown to best be calculated using the method of Mann and Kirkman (1981) for all large brown algal species investigated. This method calculates production as the product of increment and the maximal biomass of the frond (see Fig. 8.1). A recent review of techniques (Gagne and Mann 1987) in estimation of kelp productivity from growth measurements claimed this as the best model available when compared three others although it may overestimate production by 20-40 %.

Further more specific questions this study has engendered are;

#### The Coastal Environment

-are oceanic parameters as determined by satellite imagery a good means of determining prevailing water conditions in the inshore areas?

How does the nearshore nutrient environment on the north coast differ from the east south and west and what effect is this likely to have on macroalgal growth and productivity?

How significant is the effect of warmer waters including the EAC on the inshore coastal environment?

What is the effect of destructive water motion on long term community productivity?

-How does the nitrogen content of the plants correlate with the nitrogen content of the water?

#### *Durvillaea*

-What is the seasonality and productivity of the *Durvillaea* communities?

#### *Ecklonia*

-how significant is the effect of water motion on lamina length, lateral density, spinousness and corrugations?

### Macrocystis

-what is the relationship between *Macrocystis pyrifera* and *M. angustifolia* and what are the environmental parameters separating the two?

### Ecklonia juveniles

-to what extent is stipe length, lateral density, 'spinousness' and corrugations genetically decided?

### Phyllospora

--the EAC and the warm winter of 1988 appear to have had a severe effect on the populations of *Phyllospora* at George II Reef-why is this so and if the incidence increases in the near future, what are the implications for community structure?

### Red algae

- similar experiments on a larger more extensive-comprehensive scale are required so as to more accurately determine productivity.

### Abalone

-Manipulation and dietary experiments are required on north coast abalone to determine cause of stunted populations.

### Herbivores

Does the large number of shellfish at Bicheno have some sort of leveraging affect on the macroalgal communities present?

## SUMMARY

Major factors affecting the growth of the macroalgae in Tasmania are likely to be;

The amount of light available, thus implicating water turbidity and depth.

Nutrient levels of the water, an effect which ties in closely with water temperature. The warmer waters of 1988 had an apparent deleterious affect on plant species investigated.

Factors were detected on timescales of seasons and from year to year. Longer term scales tie in with the 'La Nina' - 'El Nino' phenomenon.

Water movement is probably important in keeping nutrients up to the plants but heavy swell action can be destructive. At Bicheno it was believed to be a combination of swell action and sand on the reef which was believed to inhibit the macroalgae algae through scouring.

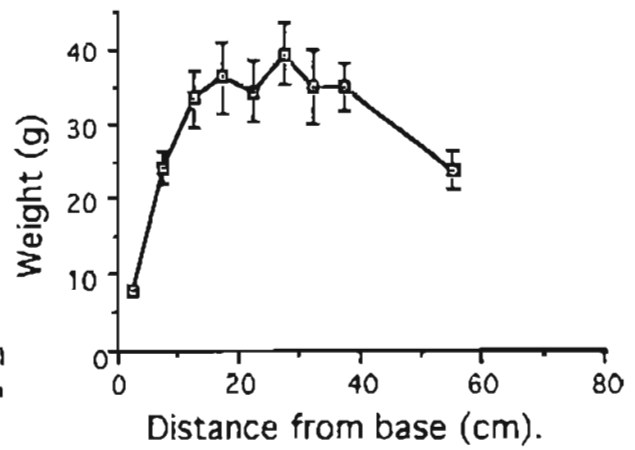
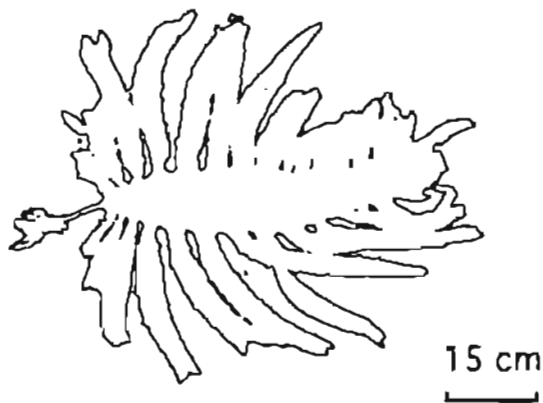
*Macrocystis* forests were also believed to have an ameliorating effect on swell dampening its destructive potential.

*Macrocystis* forests when present are a significant contributor to biomass of the inshore system. Their development should be encouraged.

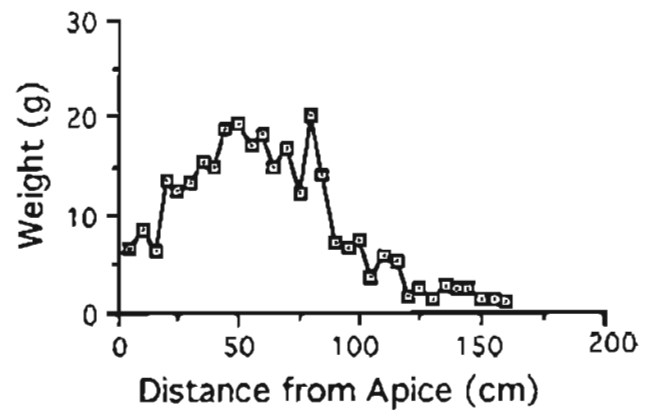
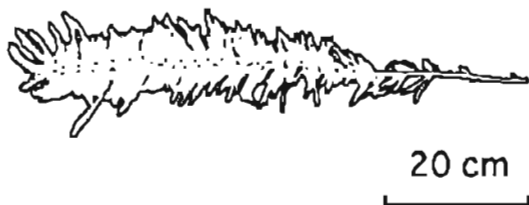
Patterns of macroalgal community development in Tasmania has many parallels with the communities off the Californian coast.

Fig. 8.1 Maximal biomass regions of the algae investigated in this study.

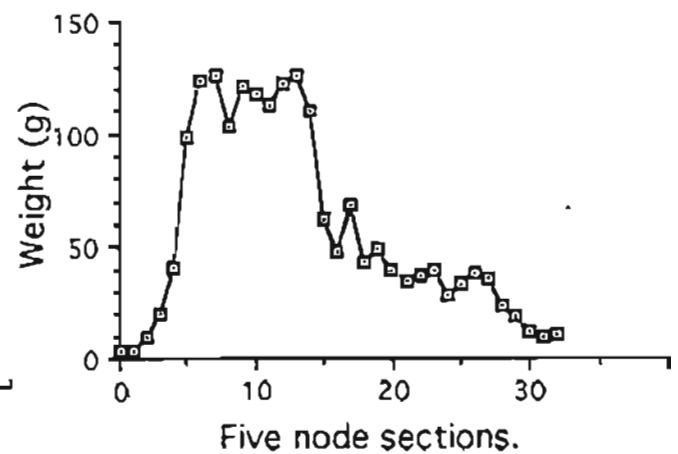
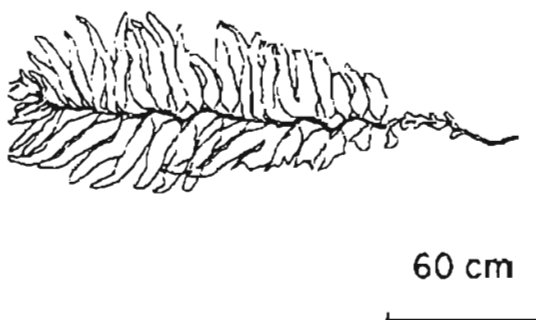
*Ecklonia radiata*



*Phyllospora comosa*



*Macrocystis pyrifera*



PART 2, CHAPTER 9.

POTENTIAL FACTORS AFFECTING ABALONE DISTRIBUTIONS IN  
TASMANIAN COASTAL WATERS.

INTRODUCTION

The initial thrust of this project was to obtain some indication of the principal factors affecting the productivity of the macroalgae in Tasmania in the hope of determining what maximal populations of abalone or sea urchins may be supported and areas where food availability is likely to be limiting. The following demonstrates how the results may be tied in with abalone biology and management.

Abalone Feeding Ecology

Five species of abalone live in distinctive habitats along the southern coast of Australia and three are of commercial importance (Shepherd 1973). The blacklip abalone, *Haliotis rubra*, one of the most commercially valuable abalone species, is distributed from the southern coast of Western Australia to the northern coast of New South Wales. This species is particularly abundant in the waters of Victoria and Tasmania.

South Australian and Victorian blacklip abalone are almost exclusively drift feeders, but capable of grazing on attached algae when drift algae are in short supply. Shepherd (1973) found that blacklip abalone have a preference for red algae over green or brown algae. Within the red algae, the blacklip

abalone was not selective, rather it was in proportion to relative abundance of species within the local community structure.

In an ancillary study to the macroalgal and abalone work at George III Reef, the feeding ecology of the abalone was investigated as part of a Study Contract (Hyndes 1986). Twenty abalone were collected periodically throughout the year from three different habitats at George III Reef distinguished by their dominant macroalgal species. These were: *Durvillaea*, *Phyllospora* and *Macrocystis* (more correctly a 'red algal community' perhaps?). A gut fullness index and a means of analysing dietary components were formulated and classification and ordination techniques were used to distinguish between diets of the abalone from the different habitats.

Gut fullness was greatest in the *Phyllospora* and the *Macrocystis* habitats, both significantly greater than the *Durvillaea* habitat (.001 and .01 respectively). The smaller Gut Fullness Index found in abalone in the shallower waters of the *Durvillaea* habitat coincided with greater distances moved by the abalone as determined in the abalone study. Prince (1989) interpreted the greater movement as a response to hunger.

By percentage occurrence, fleshy branching Rhodophytes were the dominant group of food items in all of the stomach contents, comprising 94, 50 and 58% in the *Macrocystis*, *Phyllospora* and *Durvillaea* habitats respectively. Next were the large Phaeophytes (unrecognizable at the species or generic level in samples) at 5, 36 and 33%, then the encrusting animals: 0.9, 13.7 and 8.3%. Indicator species analysis separated the *Durvillaea* and *Phyllospora* abalone gut contents from the *Macrocystis*. Gut contents of abalone from the *Durvillaea* and *Phyllospora* habitats were distinguished by *Plocamium dilatatum* and Phaeophytes and those from the *Macrocystis* habitat by the red algae *Plocamium leptophyllum* and *Sonderopelta coriacea*.



Experience in the culture of abalone has shown the best growth rates in terms of food conversion efficiency are achieved with the red algae (Hahn 1989). A local Tasmanian abalone hatchery has found that while *Haliotis rubra* will readily eat species of Phaeophyta such as *Lessonia corrugata* and *Macrocystis pyrifera*, plants of *Ecklonia radiata*, *Phyllospora* and *Durvillaea* are not eaten. This may be due to greater concentrations of anti-herbivore chemicals such as polyphenols in these plants. They will however eat these algae if the plants are allowed to rot in their cages for prolonged periods of time (A. Cuthbertson and T. Lewis of Univalve Pty Ltd pers comm.). Thus although fresh *Durvillaea* and *Phyllospora* is not eaten, drift algae consisting of these species might be. While it may appear that the abalone are selecting for red algae for their nutritive value, they may not be eating more of the brown algae because of inherent anti-herbivore defences. This is particularly so in the shallower parts of George III Reef where little drift algae, especially the larger browns accumulate due to the flatness of the reef and the high level of wave action. It is quite likely that at George III Reef attached algae make up a large proportion of the diet as few drift algae are observed on the reef.

In light of these observations and the results above, there is no reason to believe that *Haliotis rubra* in Tasmania would not feed in a similar manner to the southern Australian animals as determined by Shepherd (1973). That is they are non-selective drift feeders, but capable of grazing on attached algae (mostly reds) when drift algae are in short supply.

### Stunted Abalone Populations

Growth of abalone can be very variable over very short distances (Prince *et al.* 1987). Abalone demonstrating very slow growth are often termed 'stunted' and in Tasmania populations may never reach legal minimum size

limits. Stunted populations in Tasmanian waters are confined to limited areas on the west, south and east coasts. On the north coast however, most abalone between Rocky Cape in north east Tasmania and Waterhouse Island in the north west have slow growth rates and maximum sizes much lower than in the rest of the state (Nash *et al.* 1989). Prince *et al.* (1987) attributed this to higher temperatures in the area.

Other stunted populations are found in areas of low water movement in the D'Entrecasteaux Channel and enclosed sheltered areas on the east coast. These also are likely to suffer from temperature extremes. As this study has shown, higher temperatures usually indicate lower nutrient concentrations and conditions not amenable to growth of macroalgae, the staple item of the diet of abalone.

Temperature itself is unlikely to be the cause of stunting. Abalone in New South Wales have demonstrated high growth rates in selected coastal areas (G. Hamer, W. Nash pers comm.) and warmer waters have generally been shown to increase growth rates in culture situations (O'Hahn 1989). It would thus appear that at least in some of the areas stunting may arise from a lack of the staple diet; macroalgae which would in turn seem to be either temperature or nutrient related.

Good evidence of stunting by lack of food availability can be found in an area on the west coast widely recognized by abalone divers as having a stunted population. This is at the back of Green Island, approximately 20 kilometres north of Port Davey in Tasmania's south west. Rocks in the area experience strong currents and are bare of all macroalgae apparently due to the scouring affect of sand. It would appear that in this instance, lack of food has led to a stunted population as abalone in the south-west generally exhibit rapid growth.

The area around the Actaeon Islands in the vicinity of the site at George III Reef, anecdotally, formerly held populations of abalone at a size less than that attainable presently but in much greater concentrations (Prince per comm.). It is believed that competition between the abalone for the available food source resulted in slower growth rates and smaller abalone. As the area was progressively fished, the pressure on the available resource was lifted and resulted in more food being available to a smaller number of abalone giving increased growth rates and larger abalone. Again availability of food would appear to be a factor affecting the overall health of the population of abalone.

Generally growth rates of abalone have been shown to be fastest in the south west of Tasmania and slower in the north. Abalone divers are capable of identifying slower growing abalone (Prince *et al.* 1987) and anecdotal evidence suggests that populations of abalone more likely to be fast growing and those that aren't can be distinguished by imaginary lines on the east and west coasts (Nash pers. com.). This occurs at Gannet Point on the north west coast and in the vicinity of Bicheno and Eddystone Point on the north east coast (see Fig. 9.1). This corresponds to areas that are likely to be bathed principally by sub-antarctic waters or are adjacent to waters that may be enriched from close-by deeper waters. Gannet Point corresponds to the closest point the Continental shelf comes to on the west coast and similarly, the area between Bicheno and Eddystone Point on the east coast.

This study could not determine any substantial difference attributable to oceanic water types between the macroalgal productivities at an east coast site and a southern site. Similarly, Harris *et al.* (1987) could find little difference in the phytoplankton productivities off the west, south or east coasts, although waters of the north coast however were less productive.

Evidence thus suggests as a result of this study and other work that the stunted stocks on the north coast may at least partially so a result of lack of food through nutrient limitation. A more intensive study correlating abalone distributions and algal stocks as well as manipulation of stocks between areas differing in macroalgal communities may go some way towards answering this question.

## SUMMARY

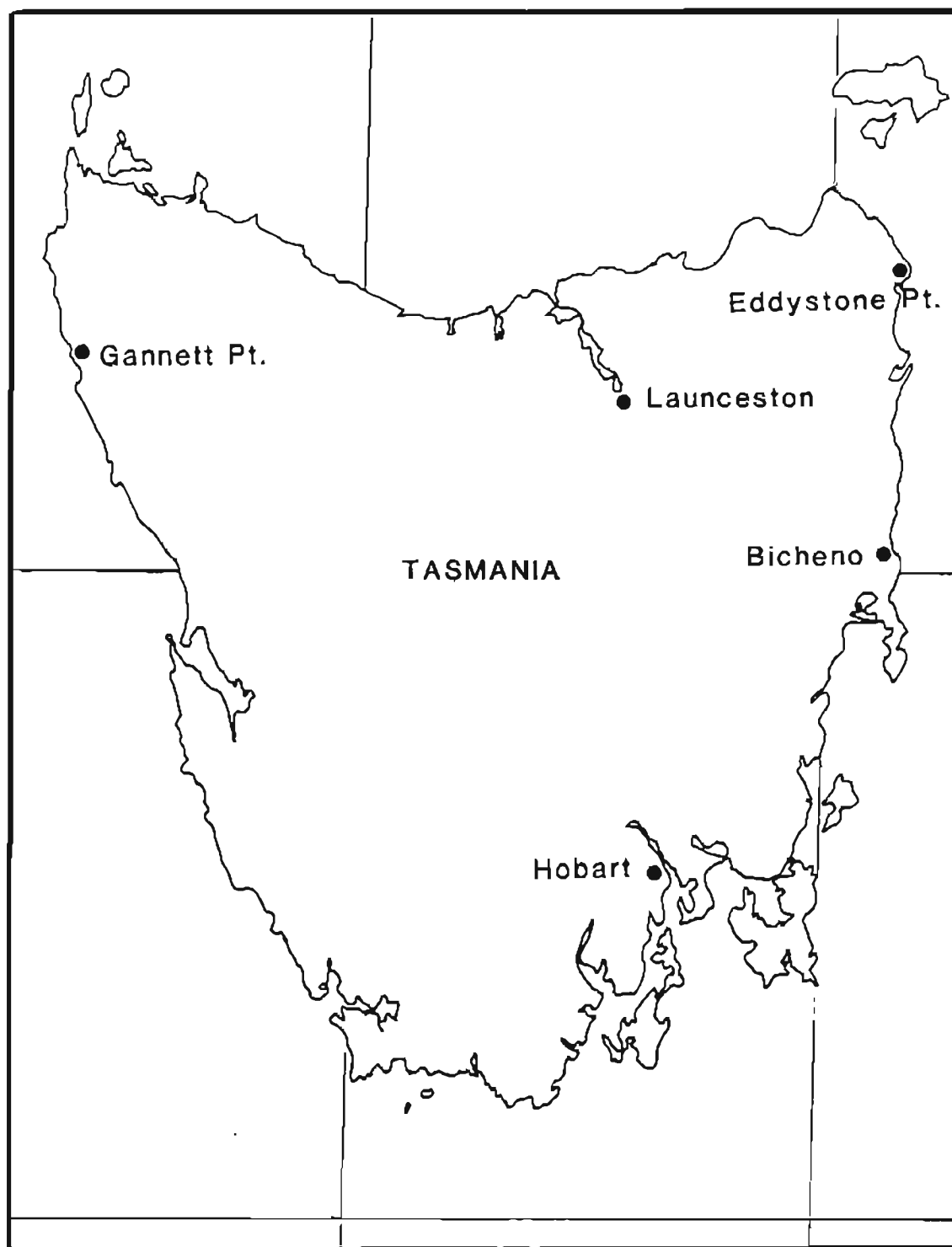
Evidence suggests that the southern Tasmanian *Haliotis rubra* are non-selective drift feeders, but capable of grazing on attached macroalgae (mostly reds) when drift algae is in short supply.

From this study, it is believed that levels of open-ocean coastal macroalgal productivity from at least Gannet Point on the west coast south to the area between Bicheno and Eddystone Point on the east coast are not likely to differ greatly.

The stunted populations of abalone in the north coast of Tasmania may be food limited as a result of nutrient depleted waters, but evidence is as yet inconclusive.

Manipulation and dietary experiments are required on north coast abalone to determine cause of stunted populations.

Fig. 9.1 Map showing localities mentioned in the text.



## REFERENCES

- Akiyama, K. (1965) Studies of ecology and culture of *Undaria pinnatifida* (Harv.) Sur. II. Environmental factors affecting the growth and maturation of gametophyte. *Bull. Tohoku Reg. Fish. Res. Lab.* 25: 143-170.
- Akiyama, K. and M. Kurogi. (1982) Cultivation of *Undaria pinnatifida* (Harvey) Suringar. The decrease in crops from natural plants following crop increase from cultivation. *Bull. Tokoku Reg. Fish. Res. Lab.* 44: 91-100.
- Ambrose, R.F. and B.V. Nelson (1982) Inhibition of giant kelp recruitment by an introduced brown alga. *Botanica Marina* 25: 265-267.
- Arasaki, S. and T. Arasaki. (1983) *Vegetables from the Sea*. Japan Publ. Inc., Tokyo, Japan.
- Arrhenius, O. (1921) Species and Area. *J. Ecol.* 9: 95-99.
- Asensi, A., M. Beucher and R. Delepine (1981) Etude sur la croissance et le developement de *Macrocystis pyrifera* (L.) C. Ag. aux Iles Kerguelen. Proc. 8th int. Seaweed Symp. (Bangor, 1974) A48: 279-289 [Fogg, G.E., Jones, W.E. (eds.) Marine Science Laboratory, Menai Bridge, N. Wales]
- Bardach, J.E., J.H. Rhyther and W.O. Mc Larney. (1982) *Aquaculture. The farming and husbandry of freshwater and marine organisms*. John Wiley & Sons, New York.
- Barrales, H.L. and C.S. Lobban (1975) The comparative ecology of *Macrocystis pyrifera* with emphasis on the forests of Chubut, Argentina. *J. Ecol.* 63: 657-677.
- Bolton, J.J. and R.J. Anderson (1987) Temperature tolerances of southern African *Ecklonia* species (Alariaceae: Laminariales) and of hybrids between them. *Mar. Biol.* 96: 293-297.

**Bouderesque, C. F., M. Gerbal and M. Knoepffler-Peguy. (1985 a)** L'algue japonnais *Undaria pinnatifida* (Phaeophyceae, Laminariales) en Mediterranee. *Phycologia* 24: 364-366.

**Calvert, H.E., C.J. Dawes and M.A. Borowitzka (1976)** Phylogenetic relationships of *Caulerpa* (Chlorophyta) based on comparative chloroplast ultrastructure. *J. Phycol.* 12: 149-162.

**Chapman, A.R.O. (1974)** The genetic basis of morphological differentiation in some *Laminaria* populations. *Mar. Biol.* 24: 85-91.

**Chapman, A.R.O. (1986)** Population and Community Ecology of Seaweeds. In *Advances in Marine Biology*. Eds: J.H.S. Blaxter and A.J. Southward. Academic Press. 23: 1-161.

**Chapman, A.R.O. and J.S. Craigie (1977)** Seasonal growth in *Laminaria longicruris*: relations with dissolved organic nutrients and internal reserves of nitrogen. *Mar. Biol.* 40:197-205.

**Chapman, A.R.O. and J.S. Craigie (1978)** Seasonal growth in *Laminaria longicruris*: relations with reserve carbohydrate storage and production. *Mar. Biol.* 46: 209-213.

**Chapman, V.J. and D.J. Chapman (1980)** *Seaweeds and their Uses*. Methuen Inc., Lond. and N.Y. 334 pp.

**Clementson, L.A., G.P. Harris , F.B. Griffiths and D.W. Rimmer (1989)** Seasonal and inter-annual variability in chemical and biological parameters in Storm Bay, Tasmania. 1. Physics, Chemistry and the biomass of components of the food chain. *Aust J Mar. Freshwater. Res.* 40: 25-38.

**Clendenning, K.A. (1971)** Photosynthesis and General Development in *Macrocystis*. In *The Biology of Giant Kelp Beds (Macrocystis) in California*. Ed: W.J. North. Beihefte zur Nova Hedwigia. 32: 169-196.

**Cribb, A.B. (1954a)** The algal vegetation of Port Arthur, Tasmania. *Pap. Proc. R. Soc. Tasmania.* 88: 1-44.

**Cribb, A.B. (1954b)** *Macrocystis pyrifera* (L.) Ag. in Tasmanian waters. *Aust. J. Mar. Freshwater Res.* 5: 1-34.

**Cribb, A.B. (1956)** Notes on marine algae from Tasmania. *Pap. Proc. Roy. Soc. Tasmania.* 90: 183-188.

**Critchley, A.T., W.F. Farnham, & S.L. Morrell (1983)** A chronology of new European sites of attachment for the invasive brown alga, *Sargassum muticum*. *J. Mar. Biol. Ass. U.K.* 63, 799-811.

**Darwin, C.R. (1860)** *The Voyage of the Beagle*. J.M. Dent & Sons, Ltd., London, 1906. 496 pp.

**Davis P.H. and V.H. Heywood (1963)** *Principles of angiosperm taxonomy*. Edinburgh and London: Oliver and Boyd.

**Dayton, P.K. (1985)** Ecology of Kelp Communities. *Ann. Rev. Ecol. Syst.* 16: 214-245.

**Dayton, P.K., V. Currie, T. Gerrodette, B. Keller, R. Rosenthal and D. Ven Tresca. (1984)** Patch dynamics and stability of some southern California kelp communities. *Ecol. Monogr.* 54: 253-289

**De Boer, J.A. (1981)** Nutrients. In *The Biology of the Seaweeds*. Ed: C.S. Lobban and M.J. Wynne. *Bot. Monogr.* 17: 356-392.

**Dean, T.A. and F.R. Jacobsen (1984)** Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. *Mar. Biol.* 83: 301-311.

**Devinny J.S. and P.D. Kirkwood (1974)** Algae associated with kelp beds of the Monterey Peninsula, California. *Bot. Mar.* 17: 100-106.

**Deysher, L.E. and T.A. Dean (1986)** In situ recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L.) C.A Agardh: effects of physical factors. *J. Exp. Mar. Biol. Ecol.* 103: 41-63.

**Dony, J.G. (1977)** Species area relationships in an area of intermediate size. *J. Ecol.* 65: 475-484.



- Doty, M.S. (1971)** Measurement of water movement in reference to benthic algal growth. *Bot. Mar.* 14: 32-35.
- Druehl, L.D. (1978)** The distribution of *Macrocystis integrifolia* in British Columbia as related to environmental parameters. *Can. J. Bot.* 56: 69-79.
- Druehl, L.D. (1984)** Morphological and physiological responses of *Macrocystis pyrifera* to nitrate enrichment. *Hydrobiologia.* 116-117: 471-474
- Ducker, S.C. (1981)** A history of Australian marine phycology. In *Marine Botany, an Australasian Perspective*. Eds: M.N. Clayton and R.J. King. Longman Cheshire Pty Ltd pp 1-14.
- Edgar G.J. (1981)** An initial survey of potential marine reserves in Tasmania. *Natl Parks Wildl. Serv. Occ. Paper.* 4: 87 pp.
- Edgar G.J. (1983a)** The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. *J. Exp. Mar. Biol. Ecol.* 70: 129-157.
- Edgar G.J. (1983b)** The ecology of south-east Tasmanian phytal animal communities. II Seasonal change in plant and animal populations. *J. Exp. Mar. Biol. Ecol.* 70: 159-179.
- Edgar G.J. (1983c)** The ecology of south-east Tasmanian phytal animal communities. III. Patterns of species diversity. *J. Exp. Mar. Biol. Ecol.* 70: 181-203
- Edgar G.J. (1983d)** The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of amphithoid amphipods among algae. *J. Exp. Mar. Biol. Ecol.* 70: 205-225.
- Edgar , G.J. (1984a)** Marine Life and Potential Marine Reserves in Tasmania. *Natl Parks Wildl. Serv. Occ. Paper.* 7: 102 pp.

**Edgar, G.J. (1984b)** General features of the ecology and biogeography of Tasmanian subtidal rocky shore communities. *Pap. Proc. Roy. Soc. Tas.* 8: 173-185.

**Edgar, G.J. (1987)** Dispersal of the faunal and floral propagules associated with drifting *Macrocystis pyrifera* plants *Mar. Biol.* 95(4): 599-560.

**Edyvane, K.S. (Unpublished Hons Thesis 1981)** *Factors affecting zonation of macroalgae at Tinderbox.* Honours Thesis, department of Plant Sciences, University of Tasmania, 1981.

**Espinoza J. and A.R.O. Chapman (1983)** Ecotypic differentiation of *Laminaria longicruris* populations in relation to seawater nitrate concentration. *Mar. Biol.* 74: 213-218

**Floc'h, J.Y., R. Pajot and I. Wallentius (1991)** The Japanese brown alga *Undaria pinnatifida* on the coast of France and its possible establishment in European waters. *J. Cons. int. Explor. Mer.* 47: 379-390.

**Foster, M.S. (1975)** Algal succession in a *Macrocystis pyrifera* forest. *Mar. Biol.* 32: 313-329.

**Funahashi, S. (1974)** Distribution of marine algae in the Japan Sea, with reference to the phytogeographical positions of Vladivostock and Noto Peninsula districts. *J. Fac. Sci. Hokkaido Univ. Ser.* 5 (10): 1-31.

**Gagne J.A., K.H. Mann and A.R.O. Chapman (1982)** Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. *Mar. Biol.* 69: 91-101.

**Gagne J.A. and K.H. Mann (1987)** Evaluation of four models used to estimate kelp productivity from growth measurements. *Mar. Ecol. Prog. Ser.* 37: 35-44.

**Gerard, V.A. (1976)** *Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California.* PhD Dissertation at the University of California, Santa Cruz.

- Gerard, V.A. (1982a)** In situ rates of nitrate uptake by giant kelp *Macrocystis pyrifera* (L.) C. Agardh: Tissue differences, environmental affects, and predictions of nitrogen limited growth. *J. Exp. Mar. Biol. Ecol.* 62: 211-224.
- Gerard, V.A. (1982b)** Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low nitrogen environment. *Mar. Biol.* 66: 27-35.
- Gerard, V.A. (1982c)** In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. *Mar Biol.* 69: 51-54.
- Gerard, V.A. (1988)** Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Mar. Biol.* 97: 25-36.
- Gerard, V.A. and K.H. Mann (1979)** Growth and Production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *J. Phycol.* 15: 33-41.
- Gleason, H.A. (1922)** On the relation between species and area. *Ecology*: 3: 158-162.
- Grieg-Smith, P. (1964)** *Quantitative Plant Ecology*. Butterworths: London. 256 pp.
- Guiler, E.R. (1952)** The Marine Algae of Tasmania-Check list with localities. *Pap. Proc. R. Soc. Tas.* 86: 71-106.
- Hahn, K. O' (1989)** Handbook of Culture of Abalone and Other Marine Gastropods. CRC Press, Inc. Boca Raton, Florida.
- Hallegraeef, G., C. Bolch, B. Koerbin and J. Bryan. (1988)** Dinoflagellate spores in the ballast water of ships. *Aust. Fish. Newsl.* 47(7): 32-34.
- Harper, J.L. (1971)** *Population Biology of Plants*. Academic Press. London and Orlando.

Harris, G.P., G.G. Ganf and D.P. Thomas (1987a) Productivity, growth rates and cell size distributions of phytoplankton in the SW Tasman Sea: implications for carbon metabolism in the photic zone. *J. Plankton Res.* 9 (5): 1003-1030.

Harris, G.P., C.S. Nilsson, L.A. Clementson and D.P. Thomas (1987b) The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Aust. J. Mar. Freshwater Res.* 38: 569-590.

Harris, G.P., P. Davies, M. Nunez and G. Meyers (1988) Interannual variability in climate and fisheries in Tasmania. *Nature* (Lond.). 333: 754-757

Harris, G.P., F.B. Griffiths, L.A. Clementson, V. Lyne and H. Van der Doe (1991) Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *J. Plankton Res.* 13: 109-131.

Harvey, W.H. (1860) Algae, in Hooker J.D., *The Botany of the Antarctic Voyage. III. Flora Tasmaniae*, London. 2:282-343.

Hatcher, B.G., H. Kirkman and W.F. Wood (1987) Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. *Mar. Biol.* 95: 63-73.

Hay, C. H. (1988) An Alien Alga in Wellington Harbour. *NZ Environment* 57: 12-14.

Hay, C. H. (1990) The Dispersal of Sporophytes of *Undaria pinnatifida* by Coastal Shipping in New Zealand and Implications for Further Dispersal of *Undaria* in France. *Br. Phycol. J.* 301-313.

Hay, C.H. and P.A. Lucken. (1987) The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. *N.Z. J. Bot.* 25: 364-366.

Hayashida, F. (1977) On age and growth of a brown alga *Ecklonia cava* Kjellman forming aquatic forest. *Bull. Jpn. Soc. Sci. Fish.* 43: 1043-1052.

Hoek, C. van den. (1982) The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biol. J. Linn. Soc.* 18: 81-144.

Hopkins, B. (1955) The species-area of plant communities. *J. Ecol.* 43: 409-426.

Hulbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2): 187-211.

Hutchins, L.W. (1947) The basis for temperature zonation in geographical distribution. *Ecol. Monogr.* 17: 325-335.

Hyndes, G. (1986) Unpublished Independent Study Contract; *Feeding ecology of the blacklip abalone Haliotis rubra (Leach, 1813) in Tasmania.* Murdoch University.

Jackson, G.A. (1983) The physical and chemical environment of a kelp community. In *The effects of waste disposal on kelp communities* Ed: W Bascom. San Diego: Univ. Calif. Inst. Mar. Res.

Jackson, G.A. (1984) Internal wave attenuation by coastal kelp stands. *J. Phys. Oceanogr.* 14: 1300-1306.

Jackson, G.A. (1987) Modelling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 95: 611-624.

Jackson, G.A., D.E. James and W.J. North (1985) Morphological relationship among fronds of giant kelp *Macrocystis pyrifera* of La Jolla, California. *Mar. Ecol. Prog. Ser.* 26 (3): 261-270.

Jackson, G.A., D.E. James and W.J. North (1986) Morphological relationships among fronds of giant kelp *Macrocystis pyrifera* off La Jolla, California. *Mar. Ecol. Prog. Ser.* 26: 261-270.

Jitts, H.R. (1965) The summer characteristics of primary productivity in the Tasman and Coral Seas. *Aust. J. Mar. Freshwater Res.* 16: 151-162.

- John D.M. (1971)** The distribution and net productivity of sublittoral populations of attached macrophytic algae in an estuary on the Atlantic coast of Spain. *Mar. Biol.* 11: 90-97.
- John, D.M., D. Lieberman and M. Lieberman (1977)** A quantitative study of the structure and dynamics of benthic subtidal algal vegetation in Ghana (tropical west Africa). *J. Ecol.* 65: 497-521.
- Jones, G. and W.F. Farnham (1973)** Japweed: new threat to British coasts. *New Scientist* 60: 394-395.
- Joska, M.A.P. and J.J. Bolton (1987)** In situ measurement of zoospore release and seasonality of reproduction in *Ecklonia maxima* (Alariaceae, Laminariales). *Br. Phycol. J.* 22: 209-214.
- Kain, J.M. (1963)** Aspects of the biology of *Laminaria hyperborea* II. Age weight and length. *J. Mar.Biol. Ass. UK.* 43: 129-151
- Kain, J.M. (1964)** Aspects of the biology of *Laminaria hyperborea* III. Survival and growth of the gametophytes. *J. Mar.Biol. Ass. UK.* 44: 415-433
- Kain, J.M. (1979)** A view of the genus *Laminaria*. *Oceanogr. Mar. Biol. Ann. Rev.* 17: 101-161
- Kain, J.M. (1982)** Morphology and growth of the giant kelp *Macrocystis pyrifera* in New Zealand and California. *Mar. Biol.* 67: 143-157.
- Kain, J.M. (1986)** Plant Size and Reproductive Phenology of Six Species of Rhodophyta in Subtidal Isle of Man. *Br. Phycol. J.* 21: 129-138.
- Kain, J.M. (1989)** The seasons in the subtidal. *Br. Phycol. J.* 24: 203-215.
- Kirk, J.T.O. (1977)** Attenuation of light in natural waters. *Aust. J. Mar. Freshwater Res.* 28: 497-508.
- Kirkman, H. (1981a)** The first year in the life history and the survival of the juvenile marine macrophyte, *Ecklonia radiata* (Turn.) J Agardh *J. Exp. Mar. Biol. Ecol.* 55: 243-254.

**Kirkman, H. (1981b)** *The biology of Ecklonia radiata and other macrophytes of the sublittoral of southwestern Western Australia*. Ph.D. Thesis at the University of Western Australia. 167 pp.

**Kirkman, H. (1984)** Standing stock and production of *Ecklonia radiata* (C. Ag.) J. Agardh. *J. Exp. Mar. Biol. Ecol.* 76: 119-130.

**Kirkman, H. (1989)** Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artificial shading off Perth, Western Australia. *Aust. J. Mar. Freshwater Res.* 40: 169-179.

**Kito, H., K. Taniguchi and K. Akiyama (1981)** Morphological variation of *Undaria pinnatifida* (Harvey) Suringar-II. Comparison of the thallus morphology of cultured F1 Plants originated from parental types of two different morphologies. *Bull. Tohoku Reg. Fish. Res. Lab.* 42: 11-18.

**Knox, G.A. (1978)** Distribution patterns of southern hemisphere marine biotas: some comments on their origin and evolution. In: *Proc. Int. Symp. Mar. Biogeog. Evol. Southern Hemisphere*. 1: 43-81.

**Larkum, A.W.D. (1986)** A study of the growth and primary production in *Ecklonia radiata* (C. Ag) J. Agardh (Laminariales) at a sheltered site in Port Jackson, New South Wales. *Mar. Biol.* 96: 177-190.

**Lindauer, V.W., V.J. Chapman and M. Aitken (1961)** The Marine Algae of New Zealand. II Phaeophyceae. *Nova Hedwigia* 3: 129-350.

**Littler, M.M. and Murray, S.N. (1975)** Impact of sewerage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol.* 30: 277-291.

**Lobban, C.S. and M.J. Wynne (1981)** *The Biology of the Seaweeds*. Blackwell Scientific Publications.

**Lobban, C.S., P.J. Harrison and M.J. Duncan (1985)** *The Physiological Ecology of Seaweeds*. Cambridge University Press.



**Loewe, F. (1957)** A note on the sea water temperature at Macquarie Is. *Aust. Met. Mag.*, 19: 60-61.

**Lucas, A.H.S. (1928)** The Marine Algae of Tasmania. *Pap. Proc. Roy. Soc. Tas.* 1928: 6-27.

**Lüning, K. (1980)** Critical levels of light and temperatures regulating the gametogenesis of three *Laminaria* species (Phaeophyceae) *J. Phycol.* 16: 1-15.

**Lüning, K. (1981)** Light. In: *The Biology of Seaweeds* Eds: C.S. Lobban and M.J. Wynne. *Bot. Monographs* 17: 326-355.

**Major, G.A., G. Dal Pont, J. Kyle, and B. Newell (1972)** Laboratory techniques in marine chemistry. *Australian Commonwealth and Industrial Research Organization Division of Fisheries and Oceanography Report* 51.

**Mann, K.H. (1972a)** Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of the seaweeds. *Mar. Biol.* 12: 1-10.

**Mann, K.H. (1972b)** Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II Productivity of the seaweeds. *Mar. Biol.* 12: 199-209.

**Mann, K.H. (1982)** Seaweed Based Systems. In: *Ecology of Coastal Waters, A Systems Approach*. Studies in Ecology, Vol. 8, Blackwell Scientific Publs.

**Mann, K.H. and H. Kirkman (1981)** Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. *Aust. J. Mar. Freshwat. Res.* 32: 297-304.

**Michanek, G. (1975)** Seaweed Resources of the Ocean. *FAO Fisheries Technical Paper* 138: 1-127; map.

**Miles, A.K. and E.C. Meslow (1990)** Effects of Experimental overgrowth on survival and change in the turf assemblage of a giant kelp forest. *J. Exp. Mar. Biol. Ecol.* 135 (3): 229-242.



Nash, W., T. Sellers, S. Talbot, A. Cawthorn and W. Ford (1989) Aspects of the growth, reproduction and mortality of abalone (*Haliotis* species) in Tasmania. I. Blacklip abalone (*H. rubra*) from the north coast and the Furneaux Group of Islands. *Dept. Sea Fish., Tasmania, Tech. Rep. No. 26*.

Neushul, M. and B.W.W. Harger (1987) Nearshore kelp cultivation, yield and genetics. In: *Seaweed Cultivation for Renewable Resources* Eds K.T. Bird and P.H. Benson. Elsevier Science Publs BV Amsterdam. 69-93

North, W.J. (1961) Life span of the fronds of the giant kelp *Macrocystis pyrifera*. *Nature*. (Lond.) 190: 1214-1215.

North, W.J. (1971) The Biology of the Giant Kelp Beds (*Macrocystis*) in California. *Beih. Nova Hedwigia*. 32: 600 pp.

North, W.J. (1989) Southern California *Macrocystis* responds to La Nina. *Applied Phycology Forum* 6(1): 4.

Norton, T.A. (1976) Why is *Sargassum muticum* so invasive? *Br. Phycol. J.* 11: 197-198.

Norton, T.A., A.C. Mathieson and M. Neushul (1981) Morphology and environment. In *The Biology of Seaweeds*. Eds: C.S. Lobban and M.J. Wynne. Blackwell Scientific Publs, Oxford. 421-451.

Novacek, I. (1984a) Response of *Ecklonia radiata* (Laminariales) to light at 15°C with reference to the light budget at Goat Island Bay, New Zealand. *Mar. Biol.* 80: 263-272.

Novacek, I. (1984b) Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. *Mar. Biol.* 81: 189-197.

Novacek, I. (1984c) Response of gametophytes of *Ecklonia radiata* (Laminariales) to temperature in saturating light. *Mar. Biol.* 82 (3): 241-245.

Novacek, I., C.J. Bird and J. Mc Lachlan. (1987) Phenology and temperature tolerance of the red algae *Chondria baileyana*, *Griffithsia globifera*, and *Dasya baillouviana* in Nova Scotia. *Can. J. Bot.* 65: 57-62.

- Pace, D.R. (1972)** *Polymorphism in Macrocystis integrifolia Bory in relation to water motion*. M. Sc. Thesis, University of British Columbia. 72 pp.
- Pearse, J.S. and A.H. Hines (1979)** Expansion of a central Californian kelp forest following the mass mortality of sea urchins. *Mar. Biol.* 51: 83-91.
- Perez, R., J. Y. Lee and C. Juge. (1981)** Observations sur la biologie de l'algue japonaise *Undaria pinnatifida* (Harvey) Suringar introduite accidentellement dans l'Etang de Thau. *Sci. Peche.* 315: 1-12.
- Perez, R., R. Kaas and O. Barbaroux. (1984)** Culture experimentale de l'algue *Undaria pinnatifida* sur les cotes de France. *Sci. Peche.* 343: 3-15.
- Prentice, S.A. and J.M. Kain (1976)** Numerical analysis of subtidal communities on rocky shores. *Est. Cstl. Mar. Sci.* 4: 65-70.
- Preston, F.W. (1962)** The canonical distribution of commonness and rarity. *Ecology* 43: 185-215.
- Prince J.D., T. Sellers, W. Ford and S. Talbot. (1987)** A survey of the abalone stocks of the Kent and Hogan Groups in Bass Strait. *Dept . Sea Fish., Tasmania, Tech. Rep. No. 24*, 15 pp.
- Prince, J.D. (1989)** *The Fisheries Biology of the Tasmanian Stocks of Haliotis rubra*. Ph.D. Thesis, University of Tasmania.
- Ramus, J. (1981)** Light in photosynthesis. In *The Biology of Seaweeds* Eds C.S. Lobban and M.J. Wynne. *Bot. Monographs* Vol. 17: 458-492.
- Rochford, D.J. (1975 b)** The Physical Setting. In 'Resources of the Sea'. *Symp. R. Soc. Tasmania*, November 1974, pp. 15-27.
- Rochford, D.J. (1984)** Nitrates in Eastern Australian Coastal Waters. *Aust. J. Mar. Freshw. Res.* 35:385-397.

Rueness, J. (1989) *Sargassum muticum* and Other Introduced Japanese Macroalgae: Biological Pollution of European Coasts. *Marine Pollution Bulletin*, Volume 20 (4): 173-176.

Russell, G. (1972) Phytosociological studies on a two zone shore. I. Basic Pattern. *J. Ecol.*, 60:539-545.

Russell, G. and A.H. Fielding (1981) Individuals, populations and communities. Ed: C.S. Lobban and M.J. Wynne. *Bot Monogr.* 17: 393-420.

Saito, Y. (1962) Fundamental studies on the propagation of *Undaria pinnatifida* (Harv.) Sur. Contr. Fish. Lab. Fac. Agr. Univ. Tokyo 3: 1-101.

Saito, Y. (1975) *Undaria* In: *Advance of Phycology in Japan* (Tohida and H Hirose, eds.). pp 304-320. Junk. The Hague.

Sakai, Y. (1977) Vegetation structure and standing crop of the marine algae in the *Laminaria* bed of Otaru City, Hokkaido, Japan. *Jap. Ecol.* 27: 45-51.

Sanderson J.C. (1984) Honours Thesis: *Macroalgae of the D'Entrecasteaux Channel*. Dept. of Plant Sciences, University of Tasmania.

Sanderson J.C. (1987a) A survey of the *Macrocystis pyrifera* (L.)C. Agardh stocks on the east coast of Tasmania. *Dept . Sea Fish., Tasmania, Tech. Rep.* No. 21

Sanderson J.C. (1987b) Macroalgal study, George III Reef. *Dept . Sea Fish., Tasmania, Tech. Rep.* No. 22.

Sanderson, J.C. (1988) In: Letters to the Editor - *Aust. Mar. Sci. Bull.* 102: 13.

Sanderson J.C. (1988) Tasmanian macroalgal species and distributions from herbarium records. *Dept . Sea Fish., Tasmania, Tech. Rep.* No. 33.

Sanderson J.C. (1990) A preliminary survey of the distribution of the introduced macroalga *Undaria pinnatifida* (Harvey) Suringer on the east coast of Tasmania. *Bot. Mar.* 33: 153-157.

**Sanderson, J.C. and D.P. Thomas (1987)** Subtidal macroalgal communities in the D'Entrecasteaux Channel, Tasmania. *Aust. J. Ecol.* 12: 41-51.

**Sanderson, J.C. and R. Di Benedetto (1988)** Tasmanian Seaweeds for the Edible Market. *Dept. Sea Fish., Tasmania, Tech. Rep. No. 32*

**Sanderson, J.C. and N. Barrett (1989)** A survey of the distribution of the introduced Japanese macroalga *Undaria pinnatifida* (Harvey) Suringer in Tasmania, December 1988. *Dept. Sea Fish., Tasmania, Tech. Rep. No. 38*

**Santileces, B. and F.P. Ojeda (1984a)** Effects of canopy removal on the understory algal community structure of coastal forests of *Macrocystis pyrifera* from southern South America. *Mar. Ecol. Prog. Ser.* 14: 165-173.

**Santileces, B. and F.P. Ojeda (1984b)** Population dynamics of coastal forests of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, southern Chile. *Mar. Ecol. Prog. Ser.* 14: 175-183.

**Schiel, D.R. and M.S. Foster (1986)** The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.* 24: 265-307.

**Setchell, W.A. (1915)** The Law of Temperature Connected with the Distribution of Marine Algae. *Ann. Mo. Bot. Gard.* 2: 287-305.

**Seymour, R.J., M.J. Tegner, P.K. Dayton and P.E. Parnell (1989)** Storm Wave Induced Mortality of Giant Kelp, *Macrocystis pyrifera*, in Southern California. *Est. Cstl. Mar. Sci.* 28: 277-292.

**Shepherd S.A. (1973)** Studies on southern Australian abalone (Genus *Haliotis*). I. Ecology of five sympatric species. *Aust. J. Mar. Freshwater Res.* 24: 217-257.

**Shepherd S.A. (1980)** *The ecology of a deep red algal community off Cape Northumberland, South Australia.* Masters Thesis, University of Adelaide. 255 pp.

**Silvertown (1982)** *Introduction to Plant Population Ecology.* Longman, London and New York. 209pp.

**Snedecor, G.W. and W.G. Cochran (1980)** *Statistical Methods*. Iowa State University Press, Ames, Iowa, U.S.A. 507 pp.

**Sokal, R.R. and F.J. Rohlf (1969)** *Biometry*, 776 pp. San Francisco: W.H. Freeman and Co.

**Stein, J.R. (1973)** *Handbook of Phycological Methods; Culture Methods and Growth Measurements*. Cambridge University Press 448 pp.

**Tamura, T. (1970)** Propagation of *Undaria pinnatifida*. In: (Tamura T., ed.) 1970: *Marine aquaculture*. Washington D.C., *National Technical Information Foundation*. (English translation of Japanese Ed. 2. 1966). pp. 1-14.

**Taniguchi, K., H. Kito and K. Akiyama. (1981)** Morphological Variation of *Undaria pinnatifida* (Harvey) Suringar I. On the Difference of Growth and Morphological Characteristics of Two Types at Matsushima Bay, Japan. *Bull. Tohoku Reg. Fish. Res. Lab.* 42: 1-9.

**Thompson, J. D., C. E. Sumner and J. G. Harris (1982)** Temperature and salinity records from an aquaculture monitoring program in Tasmania, 1961 - 1981. *Tas. Dept. Sea Fish. Tech. Rep.* 3

**Tussenbroek, B.I. van (1989a)** Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falklands. *Mar. Biol.* 100: 419-430.

**Tussenbroek, B.I. van (1989b)** The life-span and survival of fronds of *Macrocystis pyrifera* (Laminariales, Phaeophyta) in the Falkland Islands. *Br. Phycol. J.* 24: 137-141.

**Tussenbroek, B.I. van (1989c)** Morphological variations of *Macrocystis pyrifera* in the Falkland Islands in relation to environment and season. *Mar. Biol.* 102: 545-556.

**Underwood, A.J. (1981)** Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19: 513-605.

- Underwood, R. (1987)** Wave Power on the Tasmanian Coast - A Naive Analysis. *The Institution of Engineers, Australia National Conference Publication* No. 87/17 pp. 376-381.
- Velimirov, B. and C.L. Griffiths (1979)** Wave-induced kelp movement and its importance for community structure. *Bot. Mar.* 22: 169-172.
- Weinberg, S. (1976)** Submarine daylight and ecology. *Mar. Biol.* 37: 291-304.
- Wheeler, P.A. and W.J. North (1980)** Effect of nitrogen supply on nitrogen content and growth rate of *Macrocystis pyrifera* (Phaeophyta) sporophytes. *J. Phycol.* 16: 577-582.
- Wheeler, P.A. and W.J. North (1981)** Nitrogen supply, tissue composition and frond growth rates for *Macrocystis pyrifera* off the coast of California. *Mar. Biol.* 64: 59-69.
- Wheeler, W.N. (1980)** Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 56: 103-110
- Wheeler, W.N. and L.M. Srivastava (1984)** Seasonal nitrate physiology of *Macrocystis integrifolia* Bory. *J. Exp. Mar. Biol. Ecol.* 76: 35-50.
- Wilkinson, M. (1974)** Investigation on the autoecology of *Eugomontia sacculata* Kornm., a shell boring alga. *J. Exp. Mar. Biol. Ecol.* 15: 19-27.
- Wilkinson, L. and G.E. Dallal (1981)** Tests of Significance in Forward Selection Regression With an F-to-Enter Stopping Rule. *Technometrics* 23 (4): 377-380.
- Willan, R.C. (1987)** The mussel *Musculista senhousia* in Australasia; another aggressive alien highlights the need for quarantine at ports. *Bull. Mar. Sci.* 41(2): 475-489.
- Williams, R.J., F.B. Griffiths, E.J. Van der Wal and J. Kelly. (1988)** Cargo vessel Ballast Water as a Vector for the Transport of Non-indigenous Marine Species. *Estuarine Coastal Shelf Sci.* 4(2): 409-420.

Womersley, H.B.S. (1959) The marine algae of Australia. *Bot. Rev.* 25: 545-614.

Womersley, H.B.S. (1981) Biogeography of Australasian marine algae. In *Marine Botany, an Australasian Perspective*. Eds: M.N. Clayton and R.J. King. Longman Cheshire, Melbourne, 292-307.

Womersley, H.B.S. (1984) *The Marine Benthic Flora of Southern Australia. Part 1*. S.A. Govt. Printer, Adelaide. 329 pp.

Womersley, H.B.S. (1987) *The Marine Benthic Flora of Southern Australia. Part 2*. S.A. Govt. Printer, Adelaide. 484 pp.

Wood, W.F. (1987a) Effect of solar ultra-violet radiation on the kelp *Ecklonia radiata*. *Mar. Biol.* 96: 143-150.

Wood, W.F. (1987b) *The influence of light and canopy structure on growth of the kelp Ecklonia radiata (C. Ag.) J. Ag.* . PhD Thesis, University of Western Australia.

Wu, C., Z. Wen, Z. Peng and J. Zhang. (1981) Preliminary study on the productivity of some marine algae. *Phycologia* 20: 118 (Abstract).

Wyrtki, K. (1960) The surface circulation in the Tasman and the Coral Seas. *Aust. CSIRO Div. Fish. Oceanogr. Tech. Pap.*: 8.

Yarish, C.P., P. Edwards and S. Casey (1979) A culture study of the salinity responses in ecotypes of two estuarine red algae. *J. Phycol.* 15: 341-346.

Yokohama, Y., J. Tanaka and M. Chihara (1987) Productivity of the *Ecklonia cava* community in a bay of Izu Peninsula on the Pacific coast of Japan. *Bot. Mag. Tokyo*. 100: 129-141.

Yoneshigue, Y. and E.C. de Oliveira (1987) Preliminary experiments on the cultivation of the brown alga *Laminaria* (Phaeophyta) Lamaroux in Brazil. *Hydrobiologia* 151/152: 381-385.

**Zhang, D.M., G.R. Miao and L.Q. Pei (1984)** Studies on *Undaria pinnatifida*. *Hydrobiologia* 116/117: 263-265.

**Zimmerman, R.C. and J.N. Kremer (1984)** Episodic nutrient supply to a kelp forest ecosystem in Southern California. *J. Mar. Res.* 42: 591-604.

**Zimmerman, R.C. and J.N. Kremer (1986)** In situ growth and chemical composition of the giant kelp, *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. *Mar. Ecol. Prog. Ser.* 27: 277-285.